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1984

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Seabird–fishery trophic interactions in eastern Pacific boundary currents: California and Peru

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1. Abstract

The nature of seabird–fishery trophic interactions is investigated by comparative and simulation studies. Peru and California have very similar fish communities, but the seabird communities are less similar. The relationship between seabirds and fisheries cannot be considered outside the context of natural patterns of forage availability. The forage base is characterized by extreme variability, serial correlation over years, geographic expansion and contraction with changes in abundance, and species replacement events. El Niño presents special reproductive and survival problems to Peruvian seabirds. Seabird impact on fish abundance may have been significant in Peru, but is probably small in California. Fisheries may reduce food availability to seabirds with subsequent decrease in reproductive success. A simulation model suggests that a variable food supply results in variable seabird abundance. Fisheries may reduce food to levels below those necessary to sustain seabird populations, but patterns of decline may easily be misinterpreted due to long trends of population increase and decrease.

2. Résumé

L'auteur examine la nature des interactions trophiques existant entre les oiseaux de mer et la pêche par des études comparatives et simulées. Le Pérou et la Californie comptent des communautés de poissons très voisines, ce qui n'est pas le cas pour celles des oiseaux de mer. Il est impossible d'étudier le rapport entre les oiseaux de mer et la pêche sans tenir compte des modes de distribution naturels et de la disponibilité de la nourriture. La source de nourriture se caractérise par une extrême variabilité, une corrélation périodique au fil des ans, une expansion et une contraction géographiques selon les fluctuations d'abondance et certains cas de remplacement d'espèces. Le courant El Niño pose des problèmes de reproduction et de survie spécialement chez les oiseaux de mer péruviens. La prédation des oiseaux de mer peut avoir eu un effet important sur l'abondance du poisson au Pérou, mais cet effet est probablement modeste en Californie. En revanche, la pêche peut réduire la disponibilité de nourriture pour les oiseaux de mer suivie d'une baisse de la réussite de la reproduction. L'application d'un modèle de simulation révèle qu'un approvisionnement de nourriture variable entraîne des fluctuations d'abondance chez les oiseaux de mer. La pêche peut réduire la disponibilité de nourriture à des niveaux inférieurs à ceux nécessaires pour soutenir les populations d'oiseaux de mer, mais les courbes de déclin des populations peuvent être facilement mal interprétées à cause des tendances à long terme d'augmentation et de baisse des populations.

3. Introduction

Fisheries can perturb trophic relationships in an ecosystem to an extent far exceeding the scope of conventional ecological experiments. However, interpretation of fishery effects is very difficult due to lack of replication or experimental control. Two methods of confronting these problems are comparative studies and simulation modelling. Comparison of fisheries and components of ecosystems may aid our understanding of those entities to the extent that they are similar, but the consequences of their differences must also be recognized. Simulation modelling is a complementary tool of great potential, especially if supported by a sound empirical basis of natural history. The model may grossly simplify fishery and ecosystem components, but the range of possibilities within that model can be fully explored by means of perfectly replicated and controlled "experiments." These two approaches are used here to examine seabird–fishery relationships in southern California and Peru.

3.1. Eastern boundary currents

Southern California is strongly influenced by the California Current, which is one of four similar ocean currents in the world. The other three of these "eastern boundary currents" are the Peru Current, the Canary Current, and the Benguela Current off southwest Africa. These currents are similar in many respects, both physical and biological. They represent the eastern limbs of major oceanic gyres, and are characterized by a wide and moderately slow equatorward flow. Characteristically, the nearshore regions of these currents are sites of coastal upwelling, whereby wind patterns combine with the effects of the earth's rotation to cause deep, cold, nutrient-rich water to be brought to the surface as large plumes. The upwelled water often supports high primary production of phytoplankton, with subsequent secondary production of zooplankton. These in turn support an abundance of higher predators such as fish and squid, and finally larger fishes, marine mammals, and seabirds. Useful reviews of eastern boundary current characteristics are given by Bakun and Parrish (1980), and Wooster and Reid (1963). The California Current has been the most thoroughly studied example, and is reviewed by Hickey (1979) and by Reid *et al.* (1958). Upwelling itself is the subject of a recent symposium edited by Richards (1981).

3.2. Species assemblages

Eastern boundary currents are characterized by remarkably consistent assemblages of pelagic fishes (Table 1). As pointed out by Bakun and Parrish (1980), this similarity suggests that the environmental processes which determine the reproductive success of these fishes are similar as well. Except for the hake (*Merluccius* spp.) and in some cases the larger jack mackerel (*Trachurus* spp.), all of the fishes in Table 1 tend to be the object of surface fisheries utilizing purse-seine technology. The collapse of the fishery for each of these surface fishes has occurred in at least one of the four current systems (see Clark 1977, Murphy 1977, Newman and Crawford 1980, Troadec *et al.* 1980, Radovich 1981). The reason for these collapses has tended to be excessive growth of fishing capacity combined with extreme natural variability of the resource. The latter subject will be discussed in the following section.

The assemblages of guano-producing seabirds breeding in eastern boundary current areas also tend to be similar, although not as similar as assemblages of fishes. Seabirds are particularly influenced by the quality of breeding sites, which may explain the paucity of species breeding in the Canary Current. The assemblages in the two areas in the southern hemisphere bear the greatest similarity, in that they share penguins and sulids (boobies and gannets). The California Current lacks these two groups, but features a large assemblage of alcids (auks, puffins, murres, guillemots) which closely parallel the penguins in many respects (Storer 1960). Pelicans are abundant off California and Peru, but the species residing off South Africa seems to have affinity for freshwater fishes rather than for coastal pelagic fishes (Burger and Cooper, this volume). Cormorants are perhaps the quintessential guano bird, the name itself being associated with the Guanay Cormorant (*Phalacrocorax bougainvillei*) of Peru. Although the dominant cormorants off Peru and South Africa feed mainly on pelagic fishes, those off California feed more on fishes associated with the bottom (Ainley *et al.* 1981). In addition to the species listed in Table 1, gulls and terns (Laridae), shearwaters (Procellariidae), and storm petrels (Hydrobatidae) commonly are associated with eastern boundary currents, as well as many other coastal habitats. Although seabirds would seem to be more geographically mobile than fishes, the fish assemblages are more consistent among the eastern boundary current systems.

The preceding discussion has purposefully excluded offshore archipelagoes. The Canary Islands and the Galapagos Islands are similarly situated at offshore and equatorward ends of their respective currents. Both are rich in tropical and open-ocean seabirds, but are not likely to be impacted by coastal pelagic fisheries due to their relative isolation from the mainland.

Table 1
Comparison of pelagic fish species in three major eastern boundary currents (from Bakun and Parrish 1980)

	California	Peru	South Africa
Anchovy	*Engraulis mordax*	*E. ringens*	*E. capensis*
Sardine	*Sardinops sagax*	*S. sagax*	*S. ocellatus*
Jack mackerel	*Trachurus symmetricus*	*T. symmetricus*	*T. trachurus*
True mackerel	*Scomber japonicus*	*S. japonicus*	*S. japonicus*
Bonito	*Sarda chiliensis*	*S. chiliensis*	*S. sarda*
Hake	*Merluccius productus*	*M. gayi*	*M. capensis*

4. The forage base

The remainder of this paper will focus on Peru and southern California. In these systems only the anchovy is small enough to be a universal forage item for seabirds. However, younger individuals of the other surface species appear in seabird diets, and of course larger seabirds can consume larger prey. Clupeoids (anchovy and sardine) are the dominant forage items, and the following discussion will treat the variability of these species as well as their interrelationships.

4.1. Temporal variability

The northern anchovy (*Engraulis mordax*) off California has been monitored closely since 1950 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) even though a substantial commercial fishery for it did not develop until the mid 1960s. The dynamics of the stock have been sufficiently studied so that satisfactory population models have been developed (Huppert *et al.* 1980, MacCall 1980*a*). The anchovy stock has shown large fluctuations in the 30 years it has been monitored by CalCOFI, but the nature of its probable variability is better demonstrated by a time segment from a long-term simulation model (Fig. 1).

The anchovy simulation model is described by Huppert *et al.* (1980). Simulated "actual" abundances are generated by random variability about the historical stock–stock relationship of CalCOFI anchovy abundance estimates. Simulated "observed" abundances include another random variable representing relative measurement error. The simulation includes effects of fishery harvest, which is governed by a quota of one-third of the excess over one million metric tons "observed" biomass.

Two properties of this time-series are especially important. The first property is extreme variability in abundance: simulated biomass varies over a 30-fold range from smallest to largest values in this segment of the simulation. Actual estimates of anchovy abundance off California increased 30-fold from 1952 to 1965 (MacCall 1980*a*), suggesting that the simulation model may even be conservative in its variability. MacCall showed the long-term variability of anchovy abundance by means of probability distributions (Fig. 2), which suggest that abundance is approximately log-normally distributed over time.

The second property of anchovy abundance is its year-to-year serial correlation. Huppert *et al.* (1980) examined the serial-correlation properties of the simulation model, and found sequential biomasses to have a correlation coefficient (r) of about 0.6. Abundant years tend to be followed by abundant years and scarce years tend to be followed by scarce years. Approximately 40% (r^2) of the variance in abundance can be explained by the previous year's abundance, and indeed this is very near the annual survival rate of anchovy biomass, which is about 45% (MacCall 1980*a*).

The Peruvian anchoveta (*Engraulis ringens*) also appears to be quite variable in abundance, but the extent of that variability is not clear. The anchoveta sustained adult biomasses of 10–25 million metric tons despite intense harvesting during the 1960s. However, after the collapse of the resource in the early 1970s, biomasses have fluctuated between 2.5 and 6 million metric tons under greatly reduced fishing pressure (Tsukayama and Alvarez 1980, 1981).

Sardine (*Sardinops sagax*) stocks in Peru and California also appear to be volatile. MacCall (1979) showed recruitment in the California sardine to be highly variable, serially correlated, and to show little compensatory *per capita* increase at depressed stock sizes. Sardines in Peru increased from negligible abundances during the decade of the anchoveta fishery to a large fishery in the early 1980s.

4.2. Geographic variability

As Murphy (1977) points out, clupeoid fish stocks typically expand and contract with changes in abundance. For example, the range of the northern anchovy off California, as indicated by the occurrence of larvae, expanded from 1952 to 1965 (Fig. 3). As a result of this expansion, the density of anchovies spawning in the nearshore region of southern California changed relatively little with respect to overall abundance. Similar patterns have been observed in Peru, where the anchoveta has contracted into local pockets along the coast, and sardines have expanded offshore (Santander 1980, 1981).

In view of the tendency of the forage base to expand and contract, location may be an important factor in productivity and stability of seabird colonies. Colonies located near the centre of the fish stock will tend to have a more constant food supply than will colonies located toward the periphery. Examples of this geographic aspect of seabird–fishery interactions are provided by the California sardine fishery, which contracted southward into southern California during the mid 1940s (Murphy 1966). Ainley and Lewis (1974) have speculated that the larger seabirds breeding at the Farallon Islands near San Francisco were severely impacted by the disappearance of sardines. Unfortunately, seabird activity at the Farallon Islands was not consistently

Figure 2
Long-term probability distributions for observed northern anchovy abundance under two levels of exploitation (from MacCall 1980*a*); I) Unfished; II) Quota of one-third of the observed adult biomass in excess of one million metric tons (*cf*. Fig. 1)

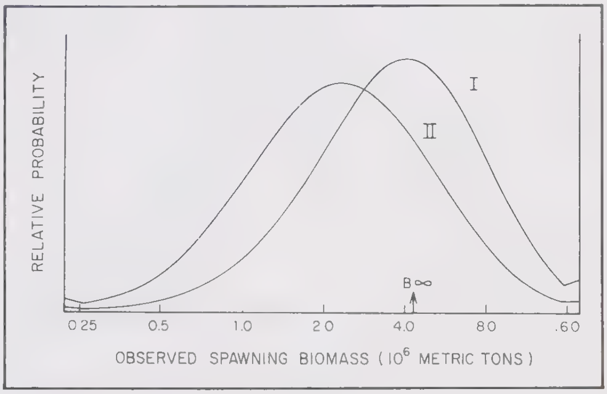


Figure 1
Simulated time series of "actual" and "observed" northern anchovy abundance (from Huppert *et al.* 1980). Dashed line is "observed" abundance below which fishery quota is zero. See text for details

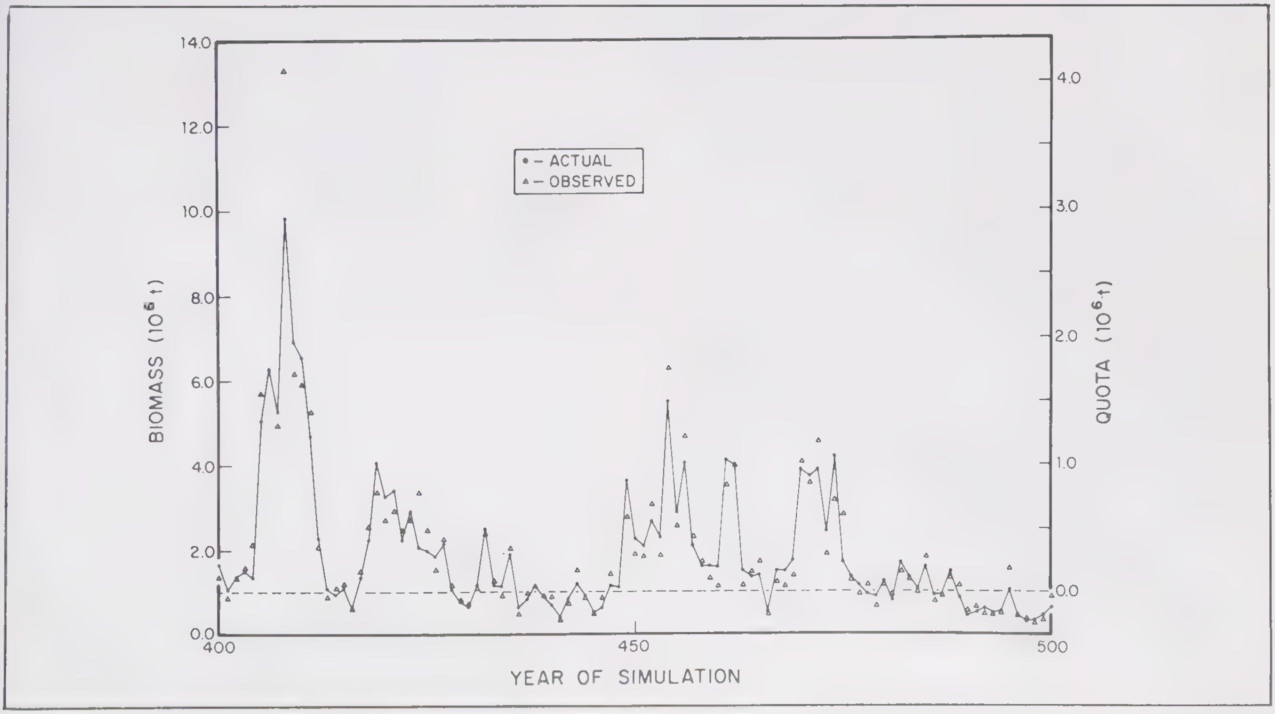
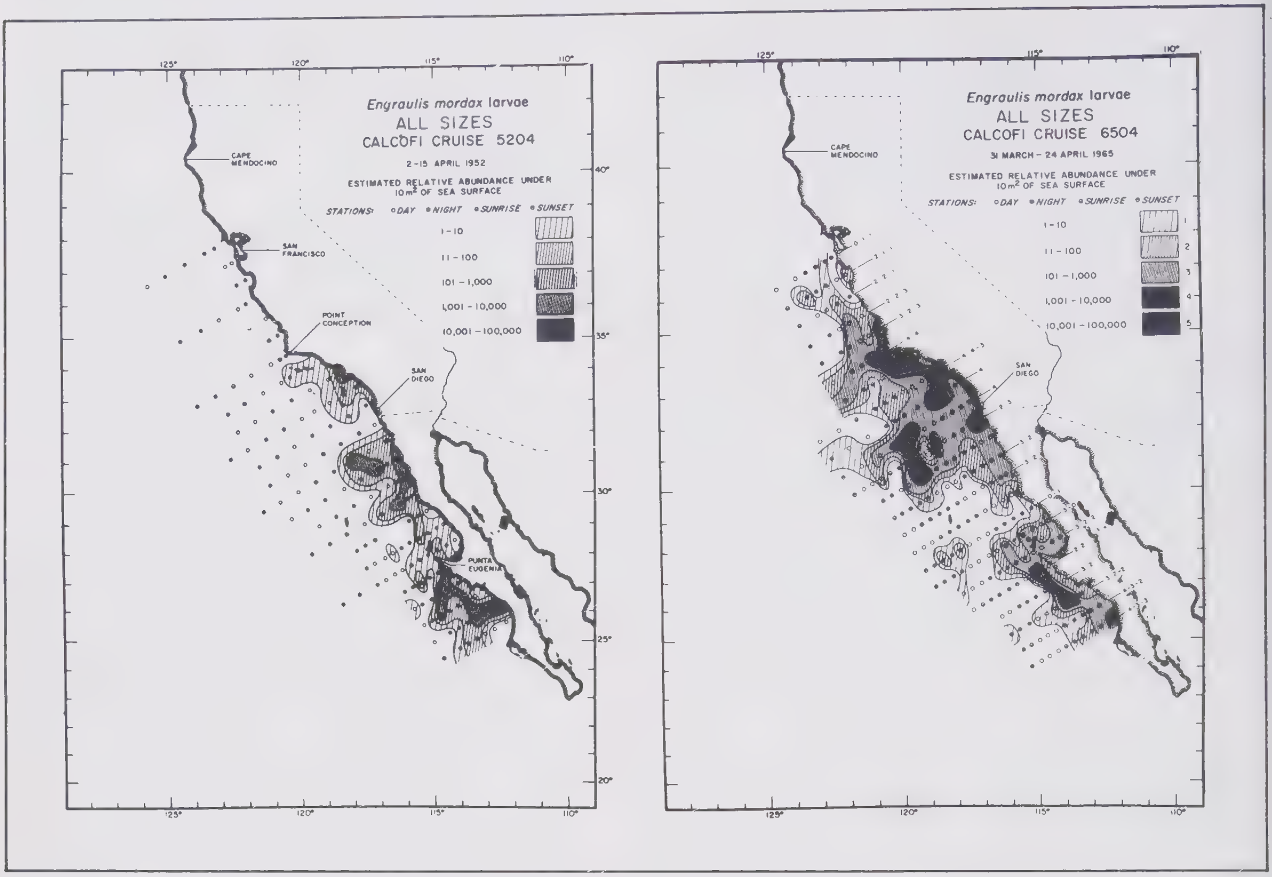


Figure 3
Geographic distribution and abundance of northern anchovy larvae at two levels of stock abundance (from Kramer and Ahlstrom 1968)


Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5204
2-15 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◉SUNRISE ◉SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
125°
120°
115°
110°
40°
35°
30°
25°
20°
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6504
31 MARCH - 24 APRIL 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: ○DAY ●NIGHT ◉SUNRISE ◉SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
1
2
3
4
5
CAPE MENDOCINO
SAN DIEGO

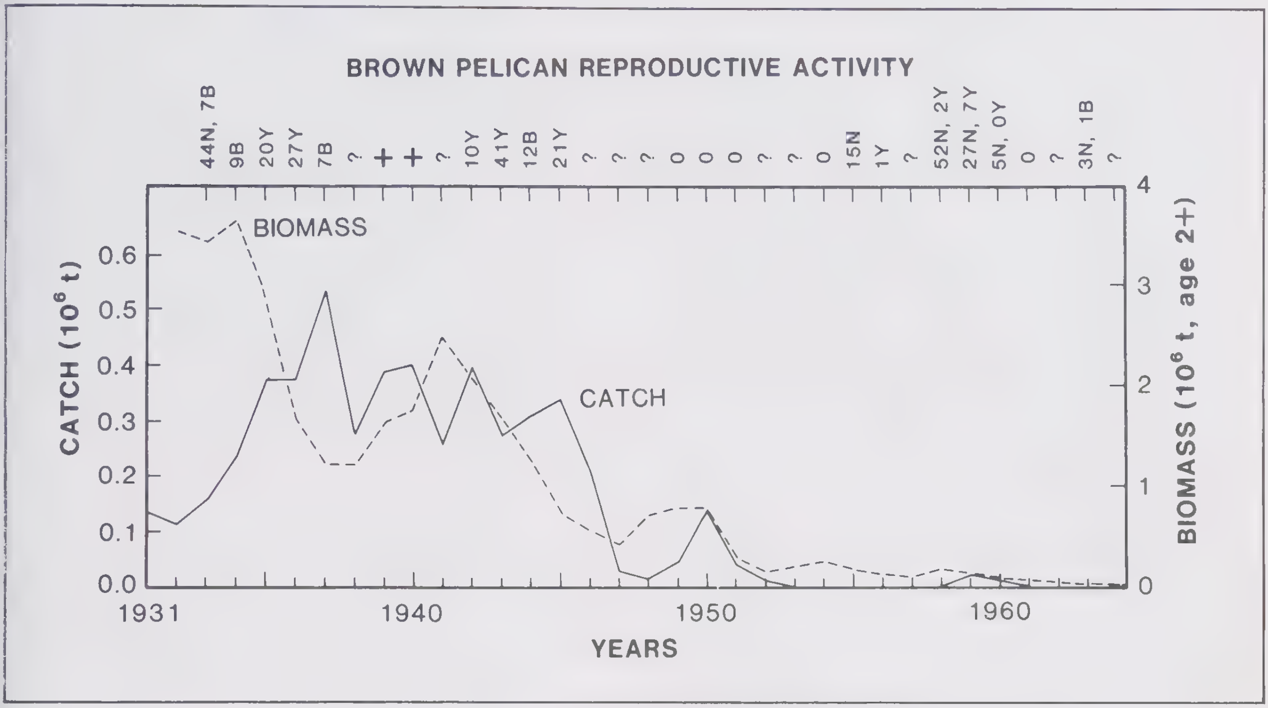
monitored until recently. A somewhat better case can be made for the Brown Pelican, (*Pelecanus occidentalis californicus*) which has sporadically nested at Point Lobos, near Monterey (Fig. 4). Baldridge (1973) has compiled a fairly continuous history of pelican breeding activity at that location since 1933. Pelican nesting activity, reproductive effort, and success roughly coincide with local sardine abundance as indicated by central California sardine fishery harvests. Although the sardine fishery continued for several years in southern California, the 1944–45 season was the last prosperous year for both the Monterey sardine fishery and the Point Lobos pelican colony. Notably, an extreme warming of the waters off California occurred during 1957–60, the so-called "warm water" period. The southern California sardine fishery briefly improved during these years, and many marine organisms extended their ranges northward (Radovich 1960, 1961). The pelican breeding attempts at Point Lobos during the late 1950s were probably associated with this warm period. The very poor success of the nesting activity was most likely due to the combination of DDT pesticide contamination (Anderson *et al.* 1975) and insufficient forage. Keith (1978) has shown that these two factors combine synergistically to severely reduce reproductive success.

4.3. Anchovy–sardine relationship

The decline of the California sardine population was followed by a large increase in anchovy abundance in southern California and to a lesser extent in central California. Murphy (1966) interpreted these trends as competitive replacement, and on the basis of goodness-of-fit, Silliman (1969) claimed to have used these data to substantiate the Lotka-Volterra competition theory. On the other hand, evidence of sardines and anchovy abundance from scale deposition rates in anaerobic sediments of a southern California basin indicated that the two species have varied similarly, rather than inversely, over the past 150 years (Soutar and Isaacs 1974). Reviews of the anchovy–sardine replacement hypothesis are given by Daan (1980) and MacCall (1980*a*).

The recent decline of anchoveta and increase of sardine in Peru has tended to strengthen the idea of replacement as a characteristic phenomenon among clupeoid fishes. Still, the mechanisms causing these changes have not been determined. Both anchovies and sardines are filter feeders, and cannibalism of their own eggs and larvae is probably the main density-dependent mechanism regulating their abundance (MacCall 1980*b*). If these two fishes

Figure 4
Brown Pelican reproductive activity at Point Lobos (Baldridge 1973) in relation to central California sardine catch (Murphy 1966) and total adult sardine biomass (Murphy 1966, MacCall 1979). Symbols: *N* = nests, *B* = broods, *Y* = young, + = some activity, 0 = no activity, ? = no observations made



inhabit the same area, they are certain to also be predators on each other's spawning products. Given the relatively low degree of compensation in the stock-recruitment relationships of these fishes, interspecific predation rather than competition is probably the mechanism governing their interaction. Such a mechanism would be expected to result in a relatively unstable relationship between the two fishes. Differential responses to exogenous influences such as environmental variability and selective fisheries may further destabilize the relationship.

Given the slow response time characteristic of anchovy–sardine replacement events, seabirds and other predators may not benefit from the relative stability usually attributed to a diverse forage base. However, the sedimentary scale record of Soutar and Isaacs (1974) suggests that maintenance of sardine–anchovy diversity may be a viable management objective. Sardine scales were present in all but one 5-year time segments in the 140 years up to 1950, but in only one segment in the 20 years following 1950. By reducing fishing pressure on either species when its abundance is low, fishery management should be able to maintain both species in at least moderate abundances, and by doing so, reduce the response time for replacement when conditions are favourable.

Anchovy–sardine replacement events have now occurred in both California and Peru. In both cases, the sardine-dominated system apparently has been centered poleward of the anchovy-dominated system. In California, the sardine fishery was largest in central California, and extended as far north as British Columbia (Murphy 1966), whereas the anchovy stocks have been most abundant in southern and Baja California (Fig. 3). In the Peruvian case, the anchoveta fishery was largest in northern and central Peru, but the recent sardine fishery has extended to southern Peru and northern Chile (G. Sharp, FAO, Rome, pers. comm.). A similar poleward shift in Peruvian fish production, although of unknown species composition, has been indicated for early historic times (Hutchinson 1950, p. 48):

> It is also noteworthy that the rather unproductive region south of Pisco Bay, as far south as Iquique [i.e. southern Peru], seems from the 16th to the early 19th centuries to have been regarded as a more important source of guano than the central Peruvian coast . . . . The only reasonable, though admittedly speculative, explanation of the decline of importance of the southern islands . . . is that minor changes in the dominant hydrographic pattern have occurred, tending to alter the distribution of the centers of abundant fish.

Evidence of sardine abundance during a period consistent with Hutchinson's speculations could be looked for in Peruvian anaerobic sediments. DeVries and Pearcy (1982: Fig. 9) found isolated sardine scales in central Peruvian coastal sediments at depths indicative of the above period.

Further investigation of Peruvian and Chilean coastal dry lakes by the methods of Goodman (1972), might elucidate the nature of these biogeographic shifts.

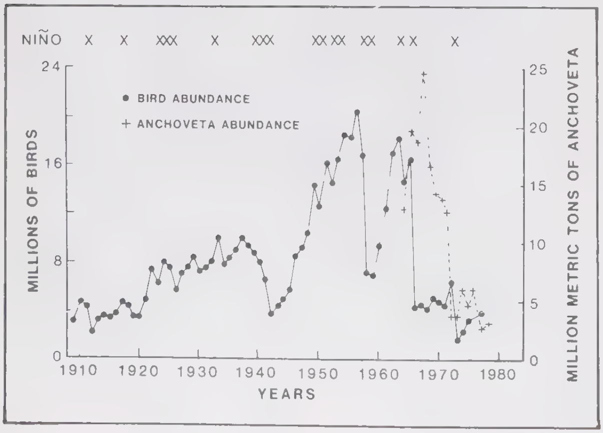
4.4. El Niño

El Niño is an oceanic condition which reaches a unique extreme in Peru. During El Niño the Peru Current episodically weakens, upwelling weakens, and the coast is flooded with warm, nutrient-poor water. A similar but less intense phenomenon occurs in other eastern boundary currents. Mechanisms and physical oceanography of El Niño are discussed by Quinn *et al.* (1978), and biological effects are discussed by Idyll (1973), Valdivia (1978), and Cushing (1981). Biological effects can be severe: reduced primary productivity may lead to fish die-offs, and ultimately to extensive mortality of seabirds, a characteristic sign of El Niño. Ashmole (1971) observes that compared to that of land birds, the life table for seabirds is characterized by low reproductive rate and high survivorship. Duffy (1980) speculates that the high food availability punctuated by severe shortages during El Niño give Peruvian seabirds an unusual life table with high reproductive rate and low survivorship.

El Niño events can be seen in the history of Peruvian guano production and/or guano-bird abundance (Fig. 5). As Idyll (1973), Duffy (1980), and others have observed, El Niño-related population declines have been more severe since the initiation of the anchoveta fishery, and population recoveries have been weak. This decrease in the resilience of the Peruvian guano birds appears to be the result of the fishery having reduced the availability of forage, both through a general reduction in anchoveta abundance, and through direct competition for available surface schools.

Hutchinson (1950:373) and Murphy (1954) have suggested that a nutrient gradient may exist in waters around guano islands, fertilizing the area, and eventually enhancing local fish abundance. This speculation takes on greater potential when El Niño conditions are considered. The Peruvian coast is normally lacking in rainfall, but during El Niño the coast may become subject to tropical downpours which have been termed "disastrous" to the guano industry (Murphy 1954), due to large amounts of guano washed into the sea. This local nutrient enrichment could be substantial under the nutrient-poor conditions of El Niño, and any attraction of fish would undoubtedly improve the foraging prospects of the seabirds inhabiting the islands, and might improve survival conditions for the fish as well. Both Hutchinson (1950) and Murphy (1954) remark that guano birds tend to retain their feces until they return to their island (although no actual evidence was given). This has usually been interpreted as contributing to improved nesting substrate, but it might also contribute to long-term forage stability and increased survivorship through the forage enhancing mechanism hypothesized above. Although this hypothesis is admittedly speculative, it could be experimentally tested by maintaining a specified minimum guano thickness on selected islands, such that the full effect of local enrichment could be observed during El Niño events (of course, fishing activity in the area would have to be restricted). Geochemical analysis, combined with past rainfall patterns could produce an estimate of optimal guano thickness, so that harvest of the excess could continue. It would indeed be ironic if overharvesting by the guano industry contributed to the collapse of the Peruvian anchoveta fishery!

Figure 5
Peruvian guano bird abundance estimated from guano production, anchoveta abundance, and occurrence of El Niño in Peru (modified from Duffy 1980, anchoveta abundance from Tsukayama and Alvarez 1980, 1981)



5. Fishery–seabird dynamics

The topic of fishery–seabird dynamics includes two fairly distinct topics: the influence of seabirds on the fishery, and the influence of the fishery on seabirds. Some aspects of these relationships have been qualitatively touched upon in the preceding discussion. The remainder of this paper will attempt to examine these relationships quantitatively.

5.1. Impact on the fishery

Furness (this volume) has reported that seabirds in several ecosystems may consume 20 to 30% of local annual pelagic fish production. This represents a potentially large increased fishery catch if numbers of birds were to be reduced. Calculations of this sort have been made for the Peruvian anchoveta fishery by Schaefer (1970), who treated the guano birds as a competing fishing fleet. Schaefer estimated that the early-fishery (i.e. 1960–63) bird population of 16 million may have consumed about 2.5 million metric tons of anchoveta per year, or about one-third the amount of the fishery. Jordan (1967) also estimated the early-fishery anchovy consumption by birds to have been between 1.8 and 2.8 million metric tons annually. This consumption rate corresponds to 28% of the initial abundance of anchoveta. This level of fish consumption is likely to have had an effect on forage abundance, and may have been a contributing factor regulating pre-fishery bird abundance. As the anchoveta fishery expanded and the bird populations declined, anchoveta harvest shifted directly from the birds and associated guano industry to the fishery.

Cushing (1981) has performed similar calculations for the quantity of anchoveta in the incoming or "recruiting" age group consumed by the seabirds. Again, the fishery catch effectively replaced anchoveta consumption by the declining seabird population. Cushing assumes the birds to have eaten mainly smaller anchoveta in the recruiting age group. This assumption is consistent with Jordan (1967) who notes that the birds consumed somewhat smaller fish than were taken by the fishery. Cushing (1981) concludes

. the change in seabird consumption of recruits distorted apparent anchoveta stock-recruitment relationship, ng a false appearance of being dome-shaped.

Consumption of fish by seabirds inhabiting the Cali- nia Current has not been fully calculated. Wiens and tt (1975) modelled the seabird–forage relationships off egon, and concluded that the birds may consume as ch as 22% of the local annual production of pelagic es. A large fraction of the total consumption was attrib- d to the numerous Sooty Shearwaters (*Puffinus griseus*) t pass along the Oregon coast during their migrations. A re ambitious attempt at calculating overall seabird con- nption of forage in the California Current was made by een (1978). Lacking precise estimates of seabird abun- ce or forage requirements, Green arrived at a tentative l seabird forage consumption of 230 000 – 630 000 t per r, with 140 000 – 380 000 t of that being small pelagic ooling fishes such as anchovy. This "educated guess" responds to less than 10% of recent anchovy biomass, ding to the conclusion that seabirds probably are not a jor source of anchovy mortality in the California Cur- t. Seabirds also consume large amounts of juvenile kfish (*Sebastes* spp.) but impact on that resource has not n quantified (Ainley *et al.* 1981).

Impact on the seabirds

Fishery impacts on seabird populations, presumably ough trophic interactions rather than direct mortality, e been inferred for Peru (Schaefer 1970, Anon. 1974, ffy 1980), and for South Africa (Crawford and Shelton 78, Burger and Cooper, this volume). Although it has g been accepted that seabird reproductive success is itive to food availability (e.g. Ashmole 1971), this tionship has been difficult to demonstrate directly, due ack of long sets of observations and difficulty in in- pendently measuring food availability. Hunt and Butler 0) have shown reproductive responses to southern fornia anchovy abundance in Western Gulls (*Larus entalis*) and in Xantus' Murrelets (*Endomychura euca*). Anderson *et al.* (1982) have shown that Brown can fledging rates in southern California vary with hovy availability. In Peru, fledging rates of guano birds ng the intense fishery, 1966–71, were half the level erved during the early fishery, 1960–63 (Anonymous 4).

Importantly, reproductive success may not vary oothly with changes in food availability. Anderson *et al.* 82) found that Brown Pelican fledging rates appear to crease sharply below a threshold level of anchovy abun- nce. Using Ringed Turtle Doves (*Streptopelia risoria*) fed to iation as controls, Keith (1978) found that if food were nited to 90% of that required for satiation, production fell 50% of the central level. Production was near zero for ds restricted to 70% of the food required for satiation. If ch a threshold response is common in seabirds, effects of wered forage availability may be very difficult to predict less the threshold level has been crossed and observed.

Animal populations are usually assumed to have me compensatory mechanism so that reproductive rates nd to increase as a response to lowered abundance. Such echanisms are poorly documented for seabirds. Ashmole 971) lists several likely mechanisms, but quantitative data e generally lacking. Again, without knowledge of com- nsatory capacity we cannot assess the resilience of seabird populations to lowered food availability and possible consequently lowered bird abundance.

5.3. A simulation model

In view of our lack of knowledge regarding the mechanisms regulating seabird reproduction and abundance, it is difficult to predict the effects that particular fisheries may have on particular seabird colonies. However, there is enough information to construct a simple simulation of a hypothetical fishery–seabird interaction. To the extent that the component processes are reasonable models, the "predictions" of the simulation model may provide useful insight into the likely nature of actual fishery–seabird interactions.

The simulation model is intended to mimic fish and seabird dynamics, exemplified by the anchovy and the Brown Pelican in southern California. The model employs several functional sub-models representing components such as age structure, reproduction, and food supply. These sub-models are arbitrary; choices of functions and parameter values are subjective. Some parameter values are constrained by others due to mathematical necessity.

The life table of the model seabird has a constant survivorship schedule, but variable *per capita* reproduction (R). The Leslie matrix, which approximates that of the California Brown Pelican (see Anderson and Gress 1983), is as follows:

$$\begin{array}{cccc}
\hline
0 & 0 & 0 & R \\
0.5 & — & — & — \\
— & 0.75 & — & — \\
— & — & 0.85 & 0.90 \\
\hline
\end{array}$$

As is shown by the right-hand column, maturity is achieved at age four years. Subadults make no reproductive contribution. All adults experience the same survivorship and reproductive success; there is no maximum age constraint, but the average remaining life span of an adult is 10 years. Birds are censused at the time of fledging, and adult abundance at that time is considered equivalent to the number that attempted breeding.

The per capita reproductive rate is determined by $R = f(F)g(N)$, where $f(F)$ denotes a function of food availability, and $g(N)$ denotes a function of bird population size. In effect, the function $g(N)$ determines the maximum possible per capita reproductive rate averaged over all adults for a given population size, and the function $f(F)$ determines what portion of that potential maximum is realized due to the constraint of food supply. Note that per capita reproduction (here termed "reproductive success") is equivalent to the number of offspring fledged per breeding pair.

Two arbitrary functions, one linear and one nonlinear, were used to model the effect of density or population size; both were calibrated to provide a replacement level of reproductive success (1.07) at a population size (N) of 1000 adults, given unlimited food availability, and to provide a maximum reproductive success (mean of all breeding birds, including survival to age one) of approximately 1.7 near zero density (Fig. 6). The parameter values chosen here are arbitrary; no special significance should be attached to them. The linear model was as follows:

$$g(N) = 1.70 - 0.00063N \text{ if } 0 < N < 2698 \text{ and}$$
$$g(N) = 0 \text{ if } N \geq 2698$$

The latter constraint is necessary to prevent negative reproductive success. The non-linear model was in the form of a "reversed" logistic curve (Fig. 6):

$$g(N) = 1.72/[1 + \mathrm{EXP}\,(0.00394N - 4.44)]$$

This shape of curve was chosen for two reasons. First, Murray (1979), Fowler (1981), and others have argued that many higher organisms, such as large mammals and birds tend to show density-dependent effects mainly at high population levels (close to carrying capacity). Second, it is unlikely that reproductive success would actually approach zero for populations in excess of carrying capacity, rather it should simply fall progressively farther below replacement.

The function used to model the effect of food availability must have a lower bound of zero, an upper bound of unity, and be capable of showing a threshold response at intermediate food levels. Again, a logistic function has these qualities (Fig. 7):

$$f(F) = 1.0/[1 + \mathrm{EXP}\,(-4.39225\,F/W)]$$

where F is a measure of food availability, scaled so that a value of $F = 0$ gives $f(F) = 0.5$. Parameter W controls the steepness of the threshold, so that if $W = 1$, $f(F)$ rises from 0.1 to 0.9 over the interval $F = [-0.5, 0.5]$, a "width" of one unit of F. Values of $W = 0.5$ and $W = 2$ reduce or expand the width of the threshold accordingly, while the centre of the response curve remains at $F = 0$.

Food availability is modelled as a serially correlated, normally distributed random variable with unit variance (Fig. 7). This simulates the approximately normal probability distribution and temporal structure seen in log-transformed anchovy abundance from previous models (Fig. 2). Serial correlation was obtained by use of the recursion algorithm (Yevdjevich 1966),

$$F_t = \rho_s F_{t-1} + r_t (1 - \rho_s^{\,2})^{1/2}$$

where F_t is log food availability in year t, ρ_s is serial correlation coefficient, and r_t is an independent normal N(0,1) random number for each year. This food-availability model does not specify whether a single-species or a multiple-species forage-base is represented. Both cases should behave similarly, except that a multiple-species forage-base may have a relatively smaller variance. It is unnecessary to consider a range of variances in the model food supply because equivalent effects can be obtained by varying the threshold steepness or "width" parameter W in the function $f(F)$.

This model of food availability has a mean value of zero. The effect of changes in mean food supply, perhaps due to fishery or other impact, is modelled by adding an appropriate constant. For example, because F is in logarithmic units, halving of the average food availability can be simulated by adding $\log_e (0.5) = -0.69$.

The model is implemented with an initial equilibrium population structure of 535, 268, 187, and 1000 for ages one, two, three, and adult respectively. As a result, random variability is not seen in the adult abundance until 4 years have elapsed. Due to the high survival rate of adults, the initial abundance of adults may influence results for decades, especially if the initial abundance is far from the eventual equilibrium.

The simulation model was used in two ways. The first way was to follow the time-course of adult bird abundance starting with initial conditions, giving a qualitative impression of patterns and trends. The second way was to determine probability distributions at long-term equilibrium. In the latter case, the simulation was run for 500 years

Figure 6
Alternative linear and non-linear models for maximum average reproductive success (function g(N), see text). Success is equivalent to the number of offspring fledged per breeding pair

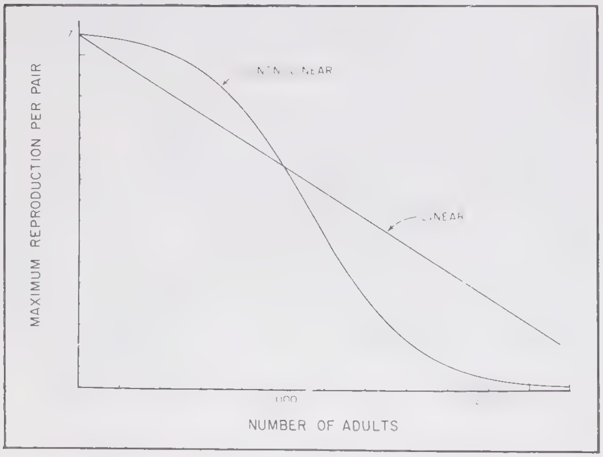
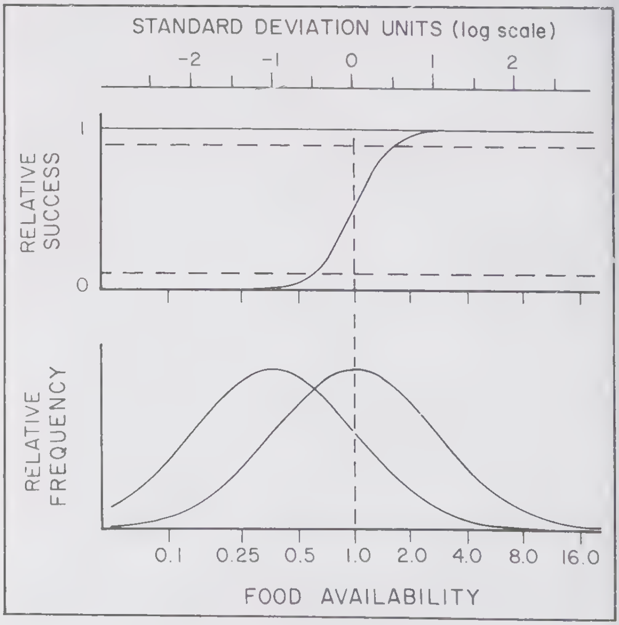


Figure 7
Upper diagram: Food availability threshold ($W = 1$) for relative reproductive success (function f(F), see text). Horizontal dashed lines are 0.1 and 0.9 levels. Lower diagram: Probability distributions of relative food availability ($\sigma_{\_} = 1$). Right probability curve represents possible virgin distribution ($\bar{F} = 1$), left probability curve represents possible distribution under exploitation ($\bar{F} = 0.37$). Note that food availability is arbitrary

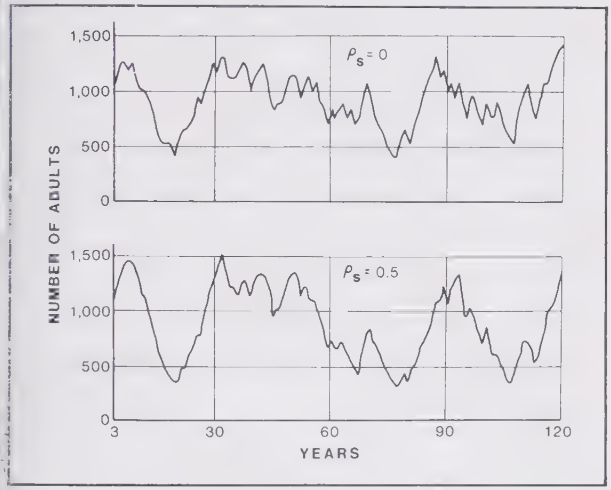


to establish equilibrium before monitoring the results. All simulations used the same series of random numbers (r_t).

5.4. Simulation results

This model was designed to investigate the fundamental question of how seabird abundance may vary as a function of characteristics of seabird food supply. Although the mean level of food availability is probably the most important factor, the variance and serial correlation of the food supply also impact the bird population.

Figure 8
Simulated time-series of seabird abundance for two levels of serial correlation (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model)



As described earlier, serial correlation is a measure of similarity of food availability in successive years. The effect of serial correlation of the food supply can be seen in comparative population trajectories (Fig. 8). Increased serial correlation preserves the overall pattern, but the excursions to high and low levels of abundance become more severe. The equilibrium probability distributions (Fig. 9) show that the bird population varies only moderately about the mean for a serially uncorrelated food supply, but in the presence of serial correlation there are occasional excursions to near-extinction. The long-term mean abundance is only slightly affected by serial correlation, as the magnitude and duration of excursions to high and low abundance nearly balance.

The effect of variance in food supply has surprisingly similar effects to those of serial correlation (Fig. 10). High variance (equivalent to a very sharp threshold) generates high population variability, whereas low variance enables the population to remain near mean abundance. Again, the effect of increased population variability is only a slight lowering of long-term mean abundance. The above simulations were for a mean food abundance centred at the mid-threshold level. Clearly, the effective variance in bird response will decrease as the mean food abundance moves above or below this threshold level. In effect, the birds will more consistently be successful or unsuccessful. If a sharp threshold response to food availability is to be expected for seabirds, these results indicate that its delineation is very

Figure 9
Long-term probability distributions of simulated seabird abundance for three levels of serial correlation, (ρ_s) in food availability ($\bar{F} = 1$, $W = 1$, $\sigma = 1$, non-linear reproduction model). The arrow indicates mean abundance

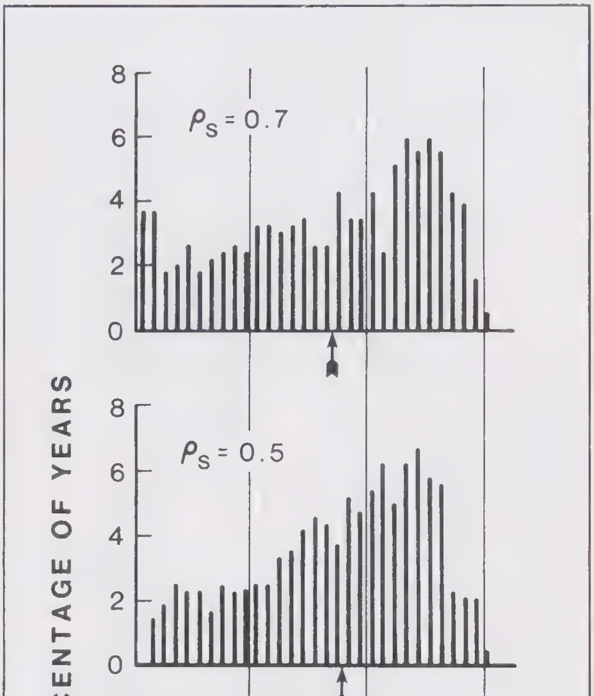
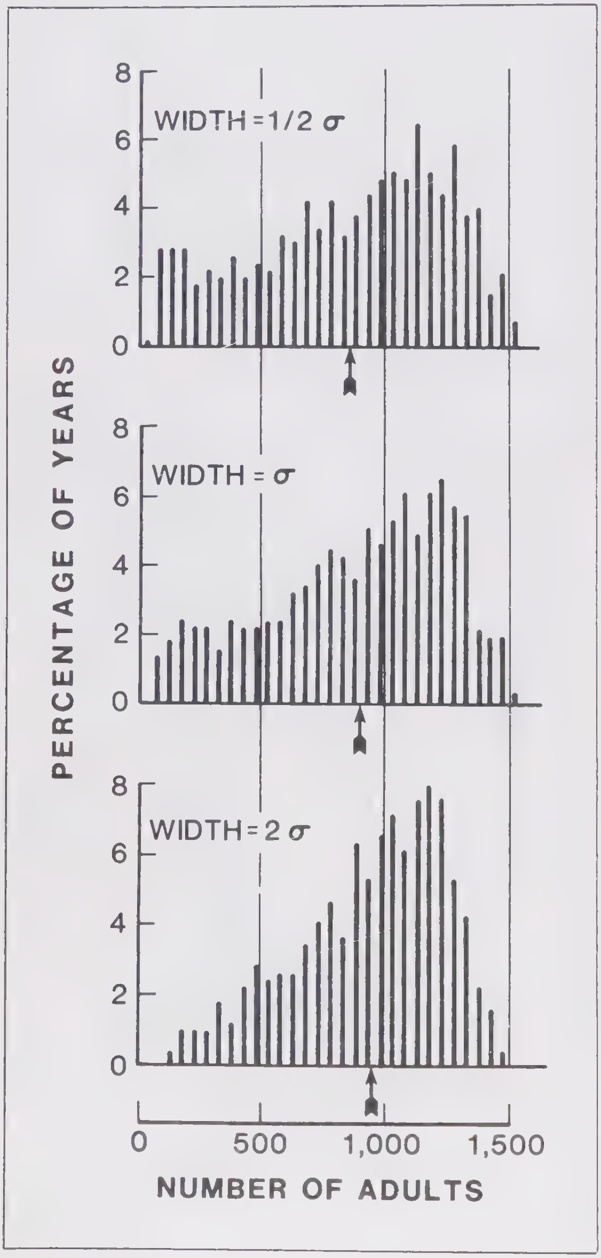


Figure 10
Long-term probability distributions of simulated seabird abundance for three threshold sensitivities (widths) to food availability ($\bar{F} = 1$, $\sigma = 1$, ρ_2, $= 0.5$, non-linear reproduction model). The arrow indicates mean abundance



Variance and serial correlation of the food supply appear to have little effect on the long-term mean bird abundance, however the mean food supply itself has the anticipated relationship to mean bird abundance. Mean bird abundance declines as mean food availability declines (Fig. 11), but there is an unexpectedly sudden drop in mean bird abundance near the critical food level causing extinction. This sharp drop is more severe for the non-linear

near the virgin level (see Fowler 1981). On an arithmetic scale, the drop is more precipitous than on the logarithmic food-availability scale of Figure 11.

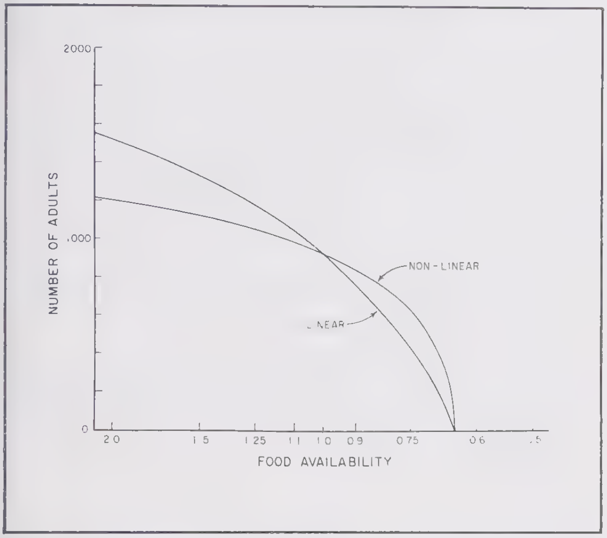
The virgin level of food abundance is defined only relatively in this model. Several possibilities can be examined. In terms of fishery impact, it is useful to assume that a "well-managed" fishery will reduce fish availability to about one-half its unexploited level. In the face of such a fishery impact, the bird population will survive if the unexploited food level is above about 1.4 relative units (Fig. 11), assuming no serial correlation of food supply. This result suggests that those seabird populations showing sporadic reproductive success under pre-fishery conditions may be severely impacted by a fishery on their food supplies. Unfortunately, many seabirds outside of Peru seem to fall into this category.

Although it is clear from Figure 11 that the model seabird can exist on a mean relative food availability of 1.0, but will become extinct on a mean food supply of 0.5, this fact would not immediately be clear from an abundance monitoring program. I simulated an example based on 120 years of seabird abundances for these two mean food levels and an initially pristine bird population: the patterns obtained were disturbingly similar (Fig. 12). Because of high serial correlation, the true long-term trend tends to be masked by prolonged variability at intermediate time scales of decades. In both cases there would be apparent cause for alarm during the first 20 years of the fishery, but the birds would stage an apparent recovery due to a more favourable environment over the subsequent 30 years. From abundance alone, it would not be apparent for over 60 years whether the population is viable. Prediction of fishery impact will require detailed studies of seabird population dynamics as well as improved fishery models. Unfortunately the long trends in seabird and fish populations associated with high serial correlations indicate that short-term studies are likely to miss upper or lower ranges of abundances which may be important to understanding long-term dynamics.

Many modifications of this simple model are possible, and until most of the reasonable cases have been examined, it would be unwise to attempt broad generalizations. It is not within the scope of this paper to attempt such a complete investigation. Other life tables have not been considered here because it would be difficult to establish a simple standard of comparison. Higher adult survival rates would require lower average reproductive success to maintain comparable population levels. However, the nature of such a change is easy to anticipate. In this model, bird abundance behaves as a moving average of fish availability, with exponentially declining weights. Higher survival would increase the span of time over which averaging occurs, and would tend to decrease the variability of seabird abundance.

Simulation modelling of a Peruvian seabird population may require three modifications. The probability distribution of the food supply should reflect sudden declines typical of El Niño; this pattern is not well modelled by the simple serial correlation algorithm used here. Also, predation pressure from the seabirds themselves might modify the availability of food. Finally, the life table would have to contain variable survival rates, perhaps dependent on food availability, to reflect the mortality that occurs during El Niño events. These investigations are beyond the scope of

Figure 11
Long-term mean simulated seabird abundance in relation to mean food availability ($\bar{F}$) for two alternative reproduction models ($W = 1, \sigma = 1, \rho_s = 0.5$, non-linear reproduction model)

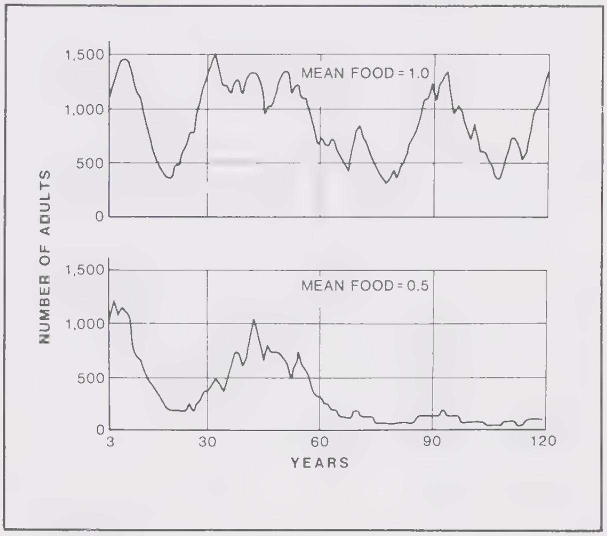


6. Conclusion

The relationship between seabird abundance and fishery activity cannot be considered outside the context of natural patterns of forage availability. Those patterns are superficially similar in California and Peru, but Peru is different in two important, interrelated respects. In the absence of an intense fishery, forage availability is much higher in Peru, but the episodic occurrence of El Niño causes more severe shortages than are observed in California. Because of these differences, the potential impacts of fisheries on seabird abundance are not necessarily comparable. The California and Peruvian fisheries are likely to impact the life table and regulatory mechanisms of the seabirds in different ways.

As more details of seabird life history and population dynamics become known, it may be possible to construct more useful models of seabird–fishery relationships. Also, improved models of the erratic temporal and geographic behaviour of the fish resources should improve the utility of seabird–fishery interaction models. The present attempt relies on an overly simple "black box" representation of these important components. The results of this exercise are suggestive, but should not be taken without reservation; yet the indication that seabirds may be slow in overall population response, but very sensitive to chronic forage depletion, should be considered in the determination of optimum fishery yields. The long life span of seabirds may allow sufficient time to gain understanding of trophic interactions so that appropriate action may be taken before species are actually endangered by prolonged reproductive difficulties. The developed countries are showing increased concern for maintaining the diversity of species in the natural environment. Let us hope that this trend reflects a movement toward human cultural maturity rather than a passing luxury allowed by inexpensive fuel and relatively abundant food

Figure 12
Simulated time-series of seabird abundance for two levels of mean food availability ($\bar{F}$ = mean food, $W = 1, \sigma = 1, \rho_s = 0.5$, non-linear reproduction model)



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QUEUING BEHAVIOR OF THE HAWAIIAN SPINY LOBSTER *PANULIRUS MARGINATUS*

Craig D. MacDonald, Stanley C. Jazwinski and James H. Prescott

Queuing behavior of spiny lobsters consists of highly stereotyped single file formations and is best known for the western Atlantic species *Panulirus argus* (Herrnkind and Cummings, 1964; Hernkind, 1969; 1977; 1980; Herrnkind and McLean, 1971, Herrnkind et al., 1973; Herrnkind and Kanciruk, 1978; Berrill, 1975; Bill and Herrnkind, 1976; Kanciruk and Herrnkind, 1976; 1978; Davis and Dodrill, 1980). Queuing in *P. argus* generally is reported in the context of extensive linear formations of up to 65 individuals that assemble inshore during a seasonal migratory phase and which move offshore. Returning queues have not been reported. The queues are noncommunal, gregarious groups in which relationships between consecutive individuals are established continually as old ones are dropped and as group membership shifts (Herrnkind et al., 1973). However, *P. argus* also forms short, aseasonal queues of just a few individuals in situations such as when deprived of shelter (Herrnkind, 1969), and when two or more individuals encounter one another over open bottom during the day (Berrill, 1975). Although there are 49 extant species of spiny lobsters (Phillips et al., 1980), heretofore queuing is described only in one species. Here we record observations of queuing in a nonmigratory lobster species, *P. marginatus* (Quoy and Gaimard, 1825) in Hawaii.

TIME SPENT IN OBSERVATIONS

The apportionment of total diver-hours of observation by diel period and geographic location during 1977–1982 is summarized in Table 1. The majority of the diving time was expended in the conduct of research on the population biology of *P. marginatus* at Kure Atoll and at French Frigate Shoals, Northwestern Hawaiian Islands. Observations rarely were made at depths exceeding 20 m.

OBSERVATIONS OF QUEUING

Queuing of *P. marginatus* was observed on two occasions in the lagoon at Kure Atoll (28°25′N, 178°20′W) and on two occasions in Kaneohe Bay at Oahu (21°30′N, 158°W) (Table 2). Respectively, these islands are situated near the northern and southern ends of the Hawaiian Archipelago. Areas where the observations occurred are sheltered from the open ocean and consist of fringing and patch reefs separated by broad stretches of silty or sandy substratum. Refer to Gross et al. (1969), Dana (1971), and Smith et al. (1973) for detailed descriptions of these areas.

In each instance, the queue consisted of two adult lobsters arranged head-to-tail as depicted for *P. argus* by Herrnkind and Cummings (1964), Herrnkind (1969), and Berrill (1975) and was highly stereotyped. Tactile contact by the antennular rami and first pereiopods of the second lobster with the extended abdomen of the lobster ahead apparently maintained queue formation. The lobsters did not feed while in the queue which appeared solely in the context of locomotion. Queues were observed once at dawn, early during the day twice, and once at night. At dawn and early during the day, lobsters were moving over open sandy bottom enroute to a patch reef when they were encountered by the diver.

Table 1. Apportionment of total diver-hours of observation (2,457 h) at different times and geographic locations in Hawaii

	Location		
Diel Period	Kure Atoll Lagoon	Kaneohe Bay, Oahu	Elsewhere in Hawaiian Archipelago*
Dawn	0	143	6
Day	1,161	279	522
Night	15	35	296

* Midway Islands, Pearl and Hermes Reef, Maro Reef, French Frigate Shoals, Necker Island, Nihoa, other locations at Oahu, Maui, and the island of Hawaii.

Upon arriving at the reef, the lobsters disengaged themselves from each other and separately acquired shelter. It was apparent, without disturbing the lobsters, that they were adults, based on their size, and that none were ovigerous females. At night, the lobsters were moving up the slope and across the top of a patch reef when encountered and captured by the diver. The leading individual was an ovigerous female of 8.5 cm carapace length and the other individual was a male of 9.5 cm carapace length. The chance encounter with each queue did not permit observation beyond about 10 min, and the duration of queuing was not determined. Although *P. marginatus* were observed in queues on only four occasions, it should be noted that the observations were made during summer, fall and spring seasons.

Queuing on shallow substrates is apparently infrequent in *P. marginatus,* judging by the few observations of queuing relative to the total number of diver-hours expended (Table 1). But queuing in this species might occur more frequently in the early evening and at dawn as lobsters leave and return to shelter while foraging at night; fewest of our diver-hours of observation were made at those times.

Discussion

Our observations of queuing in *P. marginatus* raise several questions that pertain to the adaptiveness and evolution of queuing in the Palinuridae. Queuing in spiny lobsters is thought to serve an anti-predation function (Herrnkind, 1969; Kanciruk, 1980) and to conserve energy by reducing drag during group movements (Bill and Herrnkind, 1976). Additionally, queues possibly provide a mechanism assuring appropriate orientation of the entire population during seasonal migration (Herrnkind et al., 1973; Herrnkind and Kanciruk, 1978). The results of tagging studies at Kure Atoll and French Frigate Shoals (MacDonald, unpublished data) and at Oahu (Morris, 1968) indicate that *P. marginatus* does not migrate. Instead, patterns of movement consist of home ranging behavior (*sensu* Brown and Orians, 1970) and nomadism (*sensu* Herrnkind, 1980). Since *P. marginatus* does not migrate at any of these locations, and since the hydrodynamic efficiency associated with queues of two individuals hardly differs from that of a single individual (Bill and Herrnkind, 1976), it remains that predation might be an important factor selecting for queuing in *P. marginatus.* Although the type of predator is a consideration, the greatest theoretical gain in reducing an individual's risk of predation should occur when two animals form a group (Bertram, 1978). Even in *P. argus,* queues of two individuals occur most frequently (Herrnkind et al., 1973).

The evolution of the Palinuridae has been postulated based on external morphology (George and Main, 1967), and the two species, *P. marginatus* and *P. argus,* are considered to be directly descended from a common ancestor; queuing in these species evidently is a homologous behavior. However, there appears to

Table 2. Summary information on queuing behavior of *Panulirus marginatus*

Location	Lobsters/Queue	Depth (m)	Date	Time (h)
Kure Atoll lagoon	2	5	2 June 1979	0920
Kure Atoll lagoon	2	12	11 Sept 1980	0945
Kaneohe Bay, Oahu	2	10	18 April 1978	0630
Kaneohe Bay, Oahu	2	2	5 Mar 1982	2230

be a basic difference in queuing between the two species. Whereas queuing might be adaptive as a strategy to lower the individual risk of predation in both species, it is adaptive in migration, where it affords individuals a measurable advantage in hydrodynamic efficiency, apparently only in *P. argus*. Could the apparent difference in queuing between these species thus be caused by factors that selected for migration in *P. argus* but not in *P. marginatus*?

Herrnkind (1977; 1980) suggests that the autumnal mass migration by *P. argus* in the Western Atlantic probably represented a necessary seasonal exodus, out of rapidly cooling shallows during periodic glaciations and colder periods, from which it is now emancipated, and queuing subserves a rapid, efficient exodus. In this regard, it may be significant that the large shift in the path of Gulf Stream waters caused the Atlantic in the northern hemisphere to have the highest sea-surface temperature anomaly in the world ocean between periods of extensive glaciation and the present (CLIMAP, 1976). In contrast, sea-surface temperature in Hawaii at the time that continental glaciers reached their maximum extent was calculated to differ little from the present (CLIMAP, 1976). Under these circumstances, mass queuing probably would not confer a significant selective advantage on *P. marginatus* during periodic glaciations as it may have for *P. argus*.

A better understanding of the evolution of queuing in the Palinuridae requires further observations or study of *P. marginatus* behavior. But the tendency for both *P. marginatus* and *P. argus* to form short queues when encountering other individuals over open bottom during daylight is indicated as a possible preadaptation which could have led to the evolution of the elaborate queues that function in the seasonal mass migration of *P. argus*.

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Identification of Fish Eggs

A. C. Matarese and E. M. Sandknop

A wide variety of egg types exists among teleost fishes in both freshwater and marine environments. Eggs may be pelagic and nonadhesive or demersal and either adhesive or not. They may possess a variety of specialized structures aiding in flotation or attachment. Depending on egg type and associated reproductive ecology, many characters are useful in identification. These characters have been reviewed for pelagic marine eggs by Rass (1973), Robertson (1975a), Russell (1976), and Ahlstrom and Moser (1980); we have liberally and extensively drawn from the latter. Important characters for other egg types have been discussed in part by Balon (1975a, 1981a), Hardy (1978a, b), Jones et al. (1978), and Snyder (1981). Characters such as size and possession of oil globules are important for all types; however, perivitelline space and chorion sculpturing are more important in pelagic eggs, while in demersal eggs special coatings, chorion thickness, or nature of egg deposition may be more useful.

A wealth of potential characters useful in egg identification exists; however, it is still difficult to identify eggs of most species with certainty. Except for late stages, few may be recognized at the species level. Some characters are useful at a family level, but presently it is not productive to speculate on the systematic significance of any characters (see Kendall et al., this volume). Presently, the main goal of taxonomy with respect to fish eggs is identification.

Regardless of egg type or reproductive ecology, a summary of identification characters useful to an egg taxonomist is presented. Additionally, we recommend using available literature for reference and encourage the building of local fish egg collections. We follow Ahlstrom and Ball (1954) in subdividing

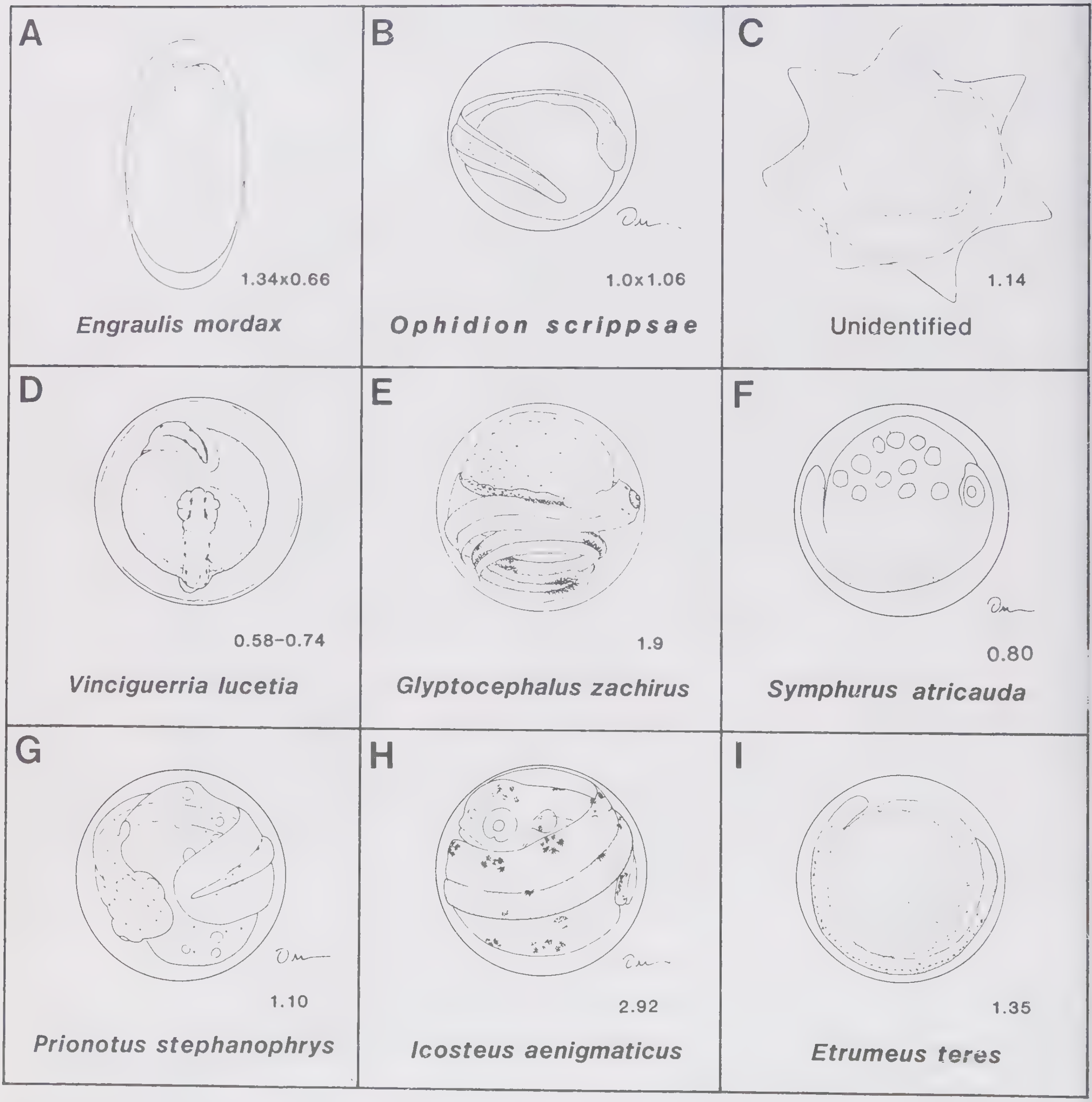
A
1.34x0.66
Engraulis mordax
B
1.0x1.06
Ophidion scrippsae
C
1.14
Unidentified
D
0.58–0.74
Vinciguerria lucetia
E
1.9
Glyptocephalus zachirus
F
0.80
Symphurus atricauda
G
1.10
Prionotus stephanophrys
H
2.92
Icosteus aenigmaticus
I
1.35
Etrumeus teres

Fig. 13. Fish eggs. Captions under each illustration indicate the species and the diameter or dimensions of the egg in millimeters. A. *Engraulis mordax*, original; B. *Ophidion scrippsae*, original; C. Unidentified, original; D. *Vinciguerria lucetia*, from Ahlstrom and Counts (1958); E. *Glyptocephalus zachirus*, from Ahlstrom and Moser (1980); F. *Symphurus atricauda*, original; G. *Prionotus stephanophrys*, original; H. *Icosteus aenigmaticus*, original; and I. *Etrumeus teres*, original.

Egg development as follows: Early—from fertilization to closure of blastopore, Middle—from closure of blastopore to tail bud lifting off yolk, and Late—from tail bud lifting off yolk to time of hatching.

Identification Characters

Shape.—The vast majority of all egg types are spherical. Exceptions include ellipsoidal eggs as found in anchovies, *Engraulis* and *Anchoa,* and slightly flattened or ovoid eggs as seen in members of the families Gobiidae, Scaridae, and Ophidiidae (Fig. 13A, B). A number of demersal eggs have somewhat irregular shapes, especially those associated with large egg masses. The perciform family Congrogadidae has cruciform shaped eggs (Herwig and Dewey, 1982). An unidentified, star-shaped egg is encountered infrequently in the Alaska region (Fig. 13C).

Size.—The average marine and freshwater fish egg size is about 1.0 mm. According to Ahlstrom and Moser (1980), pelagic fish eggs range from 0.5 mm [*Vinciguerria* (Fig. 13D)] to about 5.5 mm (Muraenidae). Demersal eggs may range higher in size (up to 7.0–8.0 mm), e.g., members of the families Salmonidae, Anarhichadidae, and Zoarcidae. Mouth brooders, e.g., in the catfish family Ariidae, have among the largest eggs with sizes from 14 mm to 26 mm.

Oil globules.—The oil globule provides useful characters in fish egg identification; these include presence or absence, number, size, position, color, and pigmentation. Among both pelagic and demersal eggs, the most common form contains a single oil globule. Eggs may lack an oil globule as in most gadines and pleuronectids (*Glyptocephalus*), contain only one (*Icosteus*), or have multiple oil globules as in the cynoglossids and triglids (*Symphurus* and *Prionotus*) (Fig. 13E, F, G, and H). In pelagic eggs with a single oil globule, the size ranges from <0.10 mm to >1.0 mm (Ahlstrom and Moser, 1980). The position of the oil globule within the yolk sac is usually posterior, but several groups contain species that have an anterior placement (e.g., orids and carangids) and others have an intermediate placement (argentinids). In some fishes, oil globules migrate during embryonic development. Some members of the family Bathylagidae initially possess multiple oil globules that eventually coalesce into a single globule (Ahlstrom, 1969). Although not a totally reliable character, the oil globule color can be useful, especially in the identification of freshly taken demersal eggs. Lastly, many species have oil globules with melanistic pigment, *Icosteus* (Fig. 13H) and *Icichthys.*

Yolk.—The degree of yolk segmentation is an important identification character. Yolk is usually segmented in primitive forms, e.g., *Etrumeus* (Fig. 13I), and homogeneous in higher forms (Rass, 1973; Ahlstrom and Moser, 1980). The opaqueness of yolk found in catfishes, salmonids, and gars can be diagnostic.[1] Pigment, which may also be diagnostic, can be present during various developmental stages from middle to late. Yolk color is often important especially in demersal eggs. Among demersal eggs vitelline circulation patterns within the yolk sac are useful in identification.[1]

Chorion.—A number of characteristics associated with the chorion or egg envelope can be useful in identifying fish eggs and have been shown to be highly adapted to the environmental conditions under which an embryo develops (Ivankov and Kurdyayeva, 1973; Stehr and Hawkes, 1979; Laale, 1980; Stehr, 1982). The most important character of the chorion is whether it is smooth, as is in most fishes, or sculptured. Among fish eggs with patterns, the size and texture (e.g., raised hexagons, pustules) of the design are diagnostic. Raised polygonal surfaces are found in several unrelated species (Stehr, 1982), e.g., *Synodus* and *Pleuronichthys* (Sumida et al., 1979), and pustules occur among some bathylagids and argentinids. *Mugil cephalus* eggs (Fig. 14A), previously considered to have a smooth chorion, have a raised patterned surface visible by scanning electron microscope (Boehlert, this volume). In many groups of fishes, the chorion has various degrees of ornamentation consisting of projections, threads, filaments, or stalks which may aid in flotation (pelagic) or attachment (demersal). In some scomberesocids, e.g., *Cololabis* (Fig. 14B), some exocoetids and atherinids, pelagic eggs are attached to each other or to a substrate by filaments. Spines are found in some myctophiforms and exocoetids, and stalks occur in some demersal egg groups, e.g., blenniids and *Osmerus mordax.* In ostraciid eggs, a patch of pustules is present near the micropyle (Fig. 14C).

Recently, thickness of the chorion has been of diagnostic value (Ivankov and Kurdyayeva, 1973; Boehlert, this volume). Stehr and Hawkes (1979), using scanning electron microscopy, found that most marine teleosts with pelagic eggs have thin chorions in relation to egg diameter whereas demersal eggs tend to develop much thicker chorions. Color of the chorion is an important diagnostic character, especially for freshly taken demersal eggs in the marine intertidal environment (Matarese and Marliave, 1982). A number of freshwater demersal fishes have eggs that possess a special coating associated with the chorion which can be either gelatinous or adhesive, e.g., *Perca, Ictalurus,* and *Notropis* (Snyder, 1981).

Perivitelline space.—Most fish eggs have a narrow- to medium-width perivitelline space, but wide spaces are common in some groups, especially among the more primitive fishes that have a segmented yolk, e.g., Clupeiformes (*Sardinops,* Fig. 14D), Anguilliformes, and Salmoniformes (*Chauliodus,* Fig. 14E) (Ahlstrom and Moser, 1980). Large perivitelline spaces are also found among some unrelated higher forms, such as cyprinids (*Notropis*), percichthyids (*Morone saxatilis*), or pleuronectids (*Hippoglossoides*).

Embryonic characters.—Characters associated with the developing embryo are extremely useful in egg identification, particularly in the middle and late stages of development. Many eggs not identifiable in the early stages are easily recognizable using embryonic characters such as pigment on embryo or finfold and morphology. In some fishes, embryonic pigment in the late stages has already undergone sufficient migration and rearrangement to the point where it resembles the yolk-sac larva; this is common in several groups including gadiformes, e.g., *Merluccius* (Fig. 14F), *Gadus,* and *Theragra,* and heavily pigmented flatfishes like *Pleuronichthys* and *Hypsopsetta.* Characteristic late-stage pigment bands appear in *Glyptocephalus* (Fig. 13E). In most freshwater species, pigment is not present prior to pigment cell migration but appears sometime after the cells have mi-

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[1] F. Douglas Martin, Chesapeake Biological Laboratory, P.O. Box 38, Solomons, Maryland 20688. Personal communication, October 1982.

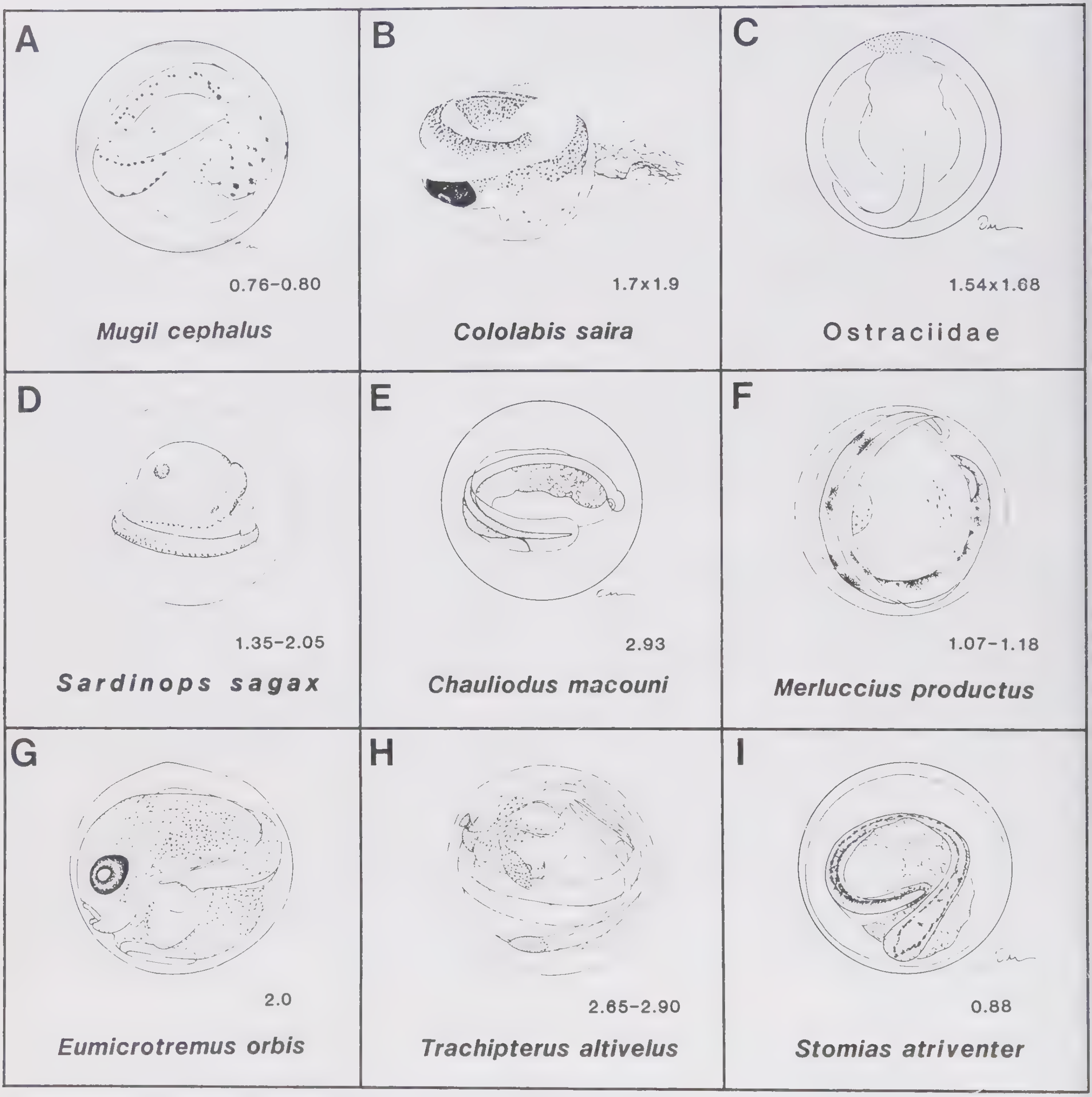
A
0.76-0.80
Mugil cephalus
B
1.7x1.9
Cololabis saira
C
1.54x1.68
Ostraciidae
D
1.35-2.05
Sardinops sagax
E
2.93
Chauliodus macouni
F
1.07-1.18
Merluccius productus
G
2.0
Eumicrotremus orbis
H
2.65-2.90
Trachipterus altivelus
I
0.88
Stomias atriventer

Fig. 14. Fish eggs. Captions under each illustration indicate the species and the diameter or dimensions of the egg in millimeters. A. *Mugil cephalus*, original; B. *Cololabis saira*, original; C. Ostraciidae, original; D. *Sardinops sagax*, original; E. *Chauliodus macouni*, original; F. *Merluccius productus*, from Ahlstrom and Counts (1955); G. *Eumicrotremus orbis*, from Matarese and Borton unpubl. MS; H. *Trachipterus altivelus*, original; and I. *Stomias atriventer*, original.

grated to their actual destinations (Snyder, 1981). As seen in the cyclopterid, *Eumicrotremus*, most late-stage demersal embryos resemble the newly hatched larva with respect to all characters (Fig. 14G). The morphology of the head, gut, and postanal body as well as the number of myomeres is used for identification within all fish egg groups. A number of specialized characters associated with the embryo are essential for identification when present, e.g., elongated fin rays—*Trachipterus* (Fig. 14H), precocious fin development (caudal—exocoetids and *Trichodon*; pelvic—*Trachinus*), and pelvic disc development in some cyclopterids (*Eumicrotremus*) (Fig. 14G).

Miscellaneous characters.—The presence of a secondary membrane inside the chorion occurs in some groups, although it is lacking in most fishes. *Stomias atriventer* eggs have a double membrane (Fig. 14I). These membranes occur in some of the more primitive fishes including members of the Anguilliformes, Clupeiformes, and Salmoniformes. In some species, like the freshwater cyprinid *Abbottina rivularis* (Nakamura, 1969), the secondary membrane is thick and gelatinous. The presence and size of the micropyle are diagnostic in other fishes, particularly freshwater demersal eggs (Laale, 1980; Riehl, 1980). Among freshwater fishes, the cleavage pattern is important for egg identification. In the more primitive families (Acipenseridae, Polyodontidae, Lepisosteidae, and Amiidae), cleavage pattern is typically semiholoblastic as opposed to the meroblastic pattern seen in the higher teleosts. Genetic studies have shown differences in LDH A zymograms to be a useful, diagnostic tool for the identification of *Gadus morhua* and *Melanogrammus aeglefinus* eggs (Mork et al., 1983).

Ecological and behavioral considerations.—A number of considerations related to mode of reproduction and collection rather than the characters of the eggs themselves are essential when identifying any type of fish egg. In identifying demersal eggs one must consider where they were collected—on rocks, on plants, in masses, and if parental care is involved. Nest type, nature of egg deposition, and the presence of guarding parents can all be essential clues to proper identification. Also, for any egg type one must note spawning time (season), location depth, and gear used for collection. In addition, the rearing of unknown eggs to an identifiable larval stage is useful in species determination as shown by Stevens and Moser (1982) for the blenny, *Hypsoblennius.* Of course, a necessary prerequisite to accurate identification of eggs is a thorough knowledge of the species present in any given area and their breeding seasonality.

SUMMARY OF CHARACTERS

Characters most useful in identification of fish eggs are the following: (1) egg shape—spherical, ellipsoidal, irregular, or otherwise; (2) egg size—fish eggs range in size from 0.5 to 26.0 mm; (3) oil globules—presence or absence, number, size, color, position, and pigmentation; (4) yolk—segmented or homogeneous, nature of segmentation, color, pigmentation, and circulation pattern; (5) chorion—smooth or ornamented, type of ornamentation, thickness, color, and coatings; (6) perivitelline space—width; (7) embryonic characters—morphological features, pigment patterns, and special structures; (8) miscellaneous characters—inner or secondary membrane (presence or absence, location), cleavage pattern, micropyle (size), and biochemical analysis; and (9) ecological and behavioral considerations—collection (gear, location, season, etc.), and mode of reproduction (nests, parental care, etc.).

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Icosteoidei: Development and Relationships

A. C. Matarese, E. G. Stevens and W. Watson

THE suborder, Icosteoidei, consists of one family, Icosteidae, with a monotypic species *Icosteus aenigmaticus* (Nelson, 1976). Adults inhabit the epi- and bathypelagic areas of the North Pacific Ocean from southern California to Japan. Adults may exceed 2 m in length and have dark flaccid bodies; a characteristic implied in the common name of the species, ragfish (Hart, 1973).

The systematic position of this group and its designation as an order or suborder is not well established. Greenwood et al. (1966) consider it a suborder of Perciformes while Gosline (1971) elevates it to an order, Icosteiformes, a probable perciform derivative.

Development

The only early life history data previously published is a brief description of the egg (Allen, 1968). *Icosteus aenigmaticus* eggs are commonly collected in ichthyoplankton surveys off the Pacific coast of North America [California Cooperative Oceanic Fisheries Investigations (CalCOFI) and Northwest and Alaska Fisheries Center (NWAFC)], but larvae (mostly preflexion) are infrequently found and a complete size series from hatching to transformation is not presently available. Larvae may move offshore or into deeper waters. The first published description and illustration of the larvae from pre- to postflexion stages are provided here, based on National Marine Fisheries Service (NMFS) collections. Although *I. aenigmaticus* juveniles undergo a marked transformation to the adult stage, little information is available concerning this change (Hart, 1973).

Eggs

The pelagic egg of *I. aenigmaticus* ranges in diameter from 2.8 to 3.1 mm (Fig. 305). A large, sometimes irregular, oil globule with a diameter of 0.42 to 0.60 mm is present. The oil globule usually decreases in size with development. The chorion is smooth, sometimes amber or rose colored. Early stage egg yolks are frequently opaque, although later stages have a clear, unsegmented yolk. During the middle stage of development, embryos have pigment along the dorsal body as well as on the yolk and oil globule. Late stage embryos have functional mouths, pectoral buds, and very wide finfolds. Scattered pigment occurs on the eyes, snout, jaws, and dorsal head. The dorsal surface of the gut is pigmented. Along the dorsal and anal finfolds, three or four clusters of melanophores appear at each distal edge. Melanophores also appear above and below the tail in the caudal finfold. An irregular double row of melanophores extends the length of the dorsal body margin. A few mediolateral spots appear anteriorly. Occasionally, pigment occurs along the ventral body margin.

Larvae

Morphology.—Newly hatched larvae of *I. aenigmaticus* are 6.5 mm NL; yolk material may persist until larvae are 10 mm. Flexion begins at about 11 mm and is complete at about 17 mm SL. The size at transformation is not known, but fin development is almost complete by 28 mm. The body, surrounded by a wide finfold, is very soft. Preflexion larvae have small heads with rounded snouts and long tapering bodies (Fig. 306). Dorsal and ventral finfolds are wider than the body. During flexion the body thickens and becomes more robust, especially anteriorly. Postflexion larvae have a robust head and gut and a tapering trunk (Fig. 306). Preanal length is less than 50% body length. A series of preopercular spines appears during late flexion.

Pigment.—Newly hatched larvae of *I. aenigmaticus* display essentially the same eye, head, gut, body, and finfold pigment as the embryos. With increasing size the head and gut usually become increasingly covered with discrete spots. Dorsal body margin pigment is present throughout larval development, while the amount of lateral and ventral body margin pigment varies and is relatively sparse. The characteristic embryonic caudal pigment persists in the developing larvae, becoming less prominent but remaining as scattered melanophores on the hypural margin and fin ray bases. In general, postflexion larvae are less pigmented except on the head. Pelvic and pectoral fin bases and pelvic rays acquire melanophores during postflexion.

Meristics.—*Icosteus aenigmaticus* larvae have the following vertebral and fin ray counts: Vert. 66–68; D 55; A 39; Pec. 21; Pel. I,4; and C 9 + 8 = 17 (NWAFC files). These counts conform

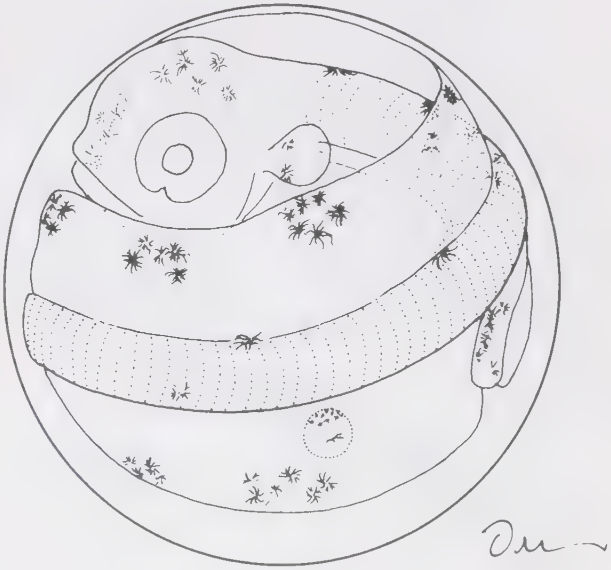

Fig. 305. Egg of *Icosteus aenigmaticus*: 2.8 mm, drawn by H. Orr.

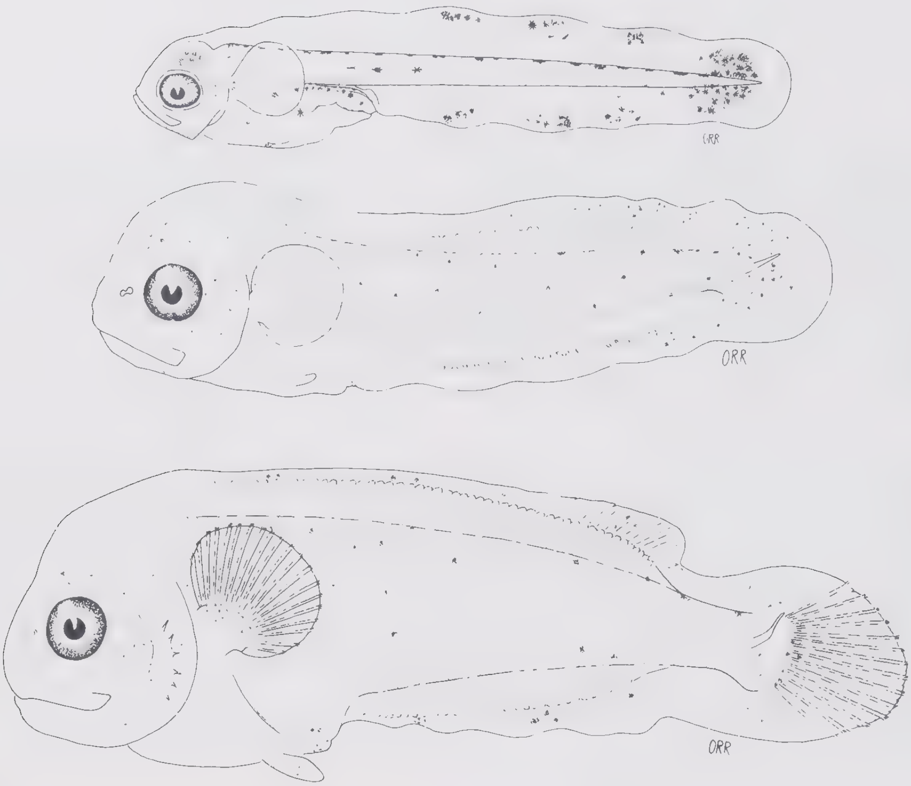

Fig. 306. Larvae of *Icosteus aenigmaticus* from top to bottom: 9.5 mm SL; 10.2 mm; and 28.5 mm SL, drawn by H. Orr.

to those for the adults except adults lack a pelvic fin (Abe, 1954; Miller and Lea, 1972; Hart, 1973). The caudal fin contains the perciform number of principal rays, 17, with 6–9 procurrent rays on each side. Pectoral fin blades are present at hatching and rays form during flexion. Pelvic fin rays begin development during flexion and are complete in postflexion larvae. At what size the pelvic fins disappear is not known. The last fin rays to form are the dorsal and anal, with their anlagen appearing in the middle of the posterior half of the finfolds at about midflexion. Formation of these fins proceeds forward and toward the body margin (Fig. 306). The largest larva available, 28.5 mm, has the complete fin ray complement.

RELATIONSHIPS

The foregoing brief description of the eggs and larvae of *I. aenigmaticus* provides some additional information toward the understanding of the life history of this unique but poorly understood fish. Characters discussed here (e.g., sequence of fin formation and meristics) help support its position among perciform relatives. Sequence of fin formation and reduced number of pelvic fin rays are blennioid-like characters, and 17 principal caudal fin rays are the typical percoid number. Eggs, larvae, and early juveniles superficially resemble stromateoid fishes but additional data are needed before a precise relationship can be determined. To understand this family more fully, we need information regarding the critical juvenile phase as well as a complete osteological examination from preflexion larvae to adults.

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Blennioidea: Development and Relationships

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The Blennioidea is composed of 16 families with about 182 genera and 759 species (Table 143). The families discussed here are those included in the infraorder Blennioidea by Nelson (1976), as amended by the current literature. For convenience we divide the infraorder into a tropical and a northern group. The tropical group is similar to Gosline's (1968) superfamily Blennioidae except for the following: 1) Ophiclinidae and Peronedysidae are synonymized with the Clinidae (George and Springer, 1980); 2) Dactyloscopidae is included (George and Springer, 1980); and 3) Congrogadidae is excluded (Winterbottom, 1982[1]). The northern group is similar to Gosline's (1968) superfamily Zoarceoidae except that we include the Bathymasteridae (Anderson, 1984). The Zoarcidae is treated separately (Anderson, this volume).

The majority of species (80%) belong to four tropical families: Tripterygiidae, Clinidae, Labrisomidae, and Blenniidae. Of the northern forms, only the family Stichaeidae represents a significant percentage (8%) of the species. Tropical Blennioidea inhabit primarily the Indo-West Pacific south to Australia, while northern fishes inhabit the North Atlantic and North Pacific (Table 143). Occasionally, representatives of mainly tropical families occur in boreal waters (e.g., Clinidae and Blenniidae), and members of northern families may occur in the subtropics. Some dactyloscopids inhabit fresh water. Four families are monotypic and three of these are endemic to the northeast Pacific.

As a group most of the 16 families in Blennioidea are not well understood, probably due to their lack of commercial importance, small size and cryptic habits. In general, the tropical and more speciose families (e.g., Blenniidae) are better known than the northern families. Monotypic families are quite poorly known. Although sparse and incomplete, some early life history information is available for 11 of the 16 families (Table 143). In most cases, however, the data on few species may not be representative of the family. Among the families in the infraorder, the Blenniidae has the greatest number of species (22) described; but with about 319 species in the family, this amounts to fewer than 10%. Morphology, pigment, and meristics of larvae in the infraorder are diverse (Figs. 302, 303).

DEVELOPMENT

Eggs

Fishes in this infraorder spawn demersal eggs (Table 144), except for some clinids. Clinids of the tribe Ophiclinini are ovoviviparous (George and Springer, 1980), while those of the tribe Clinini are viviparous (Penrith, 1969; Hoese, 1976).

Most blennioid eggs are spherical to somewhat flattened, possess one to several oil droplets, are attached to one another (and often to a substrate) by filaments or other adhesions, and have a smooth unsculptured chorion. Sizes range from among the smallest of fish eggs (Blenniidae, 0.50 mm) to among the largest (Anarhichadidae, 8.0 mm). Incubation periods range from 6 to 70 days. Eggs are unknown for four families: Xenocephalidae, Ptilichthyidae, Zaproridae, and Scytalinidae.

Parental care is common among most families; e.g., in stichaeids, males or females may guard egg masses (Shiogaki and Dotsu, 1972a; Shiogaki, 1981, 1982). In an extreme example of parental care, male dactyloscopids incubate eggs in ball-like clusters carried beneath the pectoral fins (Dawson, 1982).

Larvae

Morphological characters.—Blennioidea larvae hatch at sizes ranging from as small as 2.0 mm (Blenniidae) to as large as 17.0 mm (Anarhichadidae) (Table 145). Larvae of the northernmost families hatch at more than twice the size of larvae of the more tropical families (i.e., averaging ca. 11.5 mm versus ca. 4.5 mm). Size at which notochord flexion is complete is also variable, but tropical larvae are usually fully flexed by ca. 10.0 mm whereas northern larvae do not complete flexion until ca. 20.0 mm. At least three families have larvae with an extended pelagic existence: Blenniidae, Cryptacanthodidae, and Zaproridae. Members of the blenniid tribe, Salariini, have the only well-documented, prejuvenile pelagic stage (Miller et al., 1979; Leis and Rennis, 1983). This has been termed the "ophiblennius" stage and usually occurs between 4.6 and 26.0 mm (Fig. 302). At least two families, Cryptacanthodidae (Shiogaki, 1982) and Zaproridae (Haryu and Nishiyama, 1981), have heavily pigmented larvae and prejuveniles that are extensively collected in surface nets suggesting an extended pelagic existence (Fig. 303C, G). Most blennioid larvae do not undergo a marked metamorphosis. Transformation is usually complete in tropical forms by 26.0 mm, but may begin as early as 10.0 mm in some families (Tripterygiidae and Blenniidae). Larvae in the more northern families transform at a slightly larger size, ca. 30.0–40.0 mm, although *Ptilichthys* transforms at ca. 114.0 mm.

Among the tropical families, larval Tripterygiidae, Clinidae, and Labrisomidae share many similar morphological features. They are moderately elongate, have a preanal length about 50% BL (slightly less in labrisomids), possess a large swimbladder, and usually lack preopercular spines (Figs. 302A, B, C, D). Heads are small, sometimes rounded, with a short snout. Mouths extend just beyond the anterior eye margin. In tripterygiid and clinid larvae, the gut is initially straight but coils during flexion.

The blenniids include many larval forms with diverse morphological features. According to Leis and Rennis (1983), however, larvae are more similar within tribes than between tribes. Most species are moderately elongate (Nemophini includes both slender and robust forms), becoming either more slender (Nemophini) or more robust (Salariini) with development. Heads are short, rounded, and broad becoming more elongate with development (except Salariini larvae in which the snout elongates early in the preflexion stage). The gut is short to moderate (usually < 50% BL), and eventually coiled if not so initially. Larval preopercular spination may be elaborate: spines can be numer-

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[1] Winterbottom, R. 1982. The perciform fish family Congrogadidae—biogeography and evidence for monophyly. Amer. Soc. Ich. Herp., oral paper, 62nd annual meeting.

Table 143. General Summary and Early Life History (ELH) Information in Blennioidea.

				Early life history			
Taxon	Number of genera	Approx. number of species	Primary Distribution	Number of genera	Number of species	Number of species illustrated	Primary early life history sources
Blennioidea							
Dactyloscopidae	6	20	Atlantic, Pacific (tropical)	1	1		Dawson 1982
Xenocephalidae	1	1	New Ireland, New Guinea	0	0		
Notograptidae	2	3	Australia	0	0		
Tripterygiidae	18–19	75–95	Atlantic, Pacific, Indian (tropical)	5	6	7	Graham, 1939; Leis and Rennis, 1983; Miller et al., 1979; Ruck, 1973a, 1980; Shiogaki and Dotsu, 1973; Watson, unpubl.; Wirtz, 1978
Clinidae	26	85	Atlantic, Pacific, Australia	4	5	14	Barnhart, 1932; Padoa, 1956h; Shiogaki and Dotsu, 1972b; Sparta, 1948; Stevens, unpubl.; Watson, unpubl.
Chaenopsidae	10	55	Atlantic, Pacific (tropical)	0	0		Böhlke, 1957; Stephens et al., 1966
Labrisomidae	14	100	New World (tropical)	2	3	3	Breder, 1939; Breder, 1941; Springer, 1958; Watson, unpubl.
Blenniidae	53	289–319	Indo-Pacific	17	22	27	Cipria, 1934, 1936; Dotsu, 1982; Dotsu and Moriuchi, 1980; Dotsu and Oota, 1973; Dutt and Rao, 1960; Eggert, 1932; Fishelson, 1963, 1976; Fives, 1970a; Ford, 1922; Fritzsche, 1978; Hildebrand and Cable, 1938; Lebour, 1927; Leis and Rennis, 1983; Lippson and Moran, 1974; Miller et al., 1979; Mito, 1954; Munro, 1955; Peters, 1981; Qasim, 1956; Rao, 1970; Russell, 1976; Stevens and Moser, 1982; Thomson and Bennett, 1953; Watson, 1974, unpubl.; Wickler, 1957
Bathymasteridae	3	7	North Pacific	2	3	1	Breder and Rosen, 1966; Fitch and Lavenberg, 1975; Matarese, unpubl.
Stichaeidae	37	54	North Atlantic, Pacific	14	18	15	Breder and Rosen, 1966; Faber, 1976; Hart, 1973; Marliave, 1975; Matarese, unpubl.; Peppar, 1965; Rass, 1949; Russell, 1976; Shiogaki, 1981; Shiogaki, 1983; Shiogaki and Dotsu, 1972a; Tokuya and Amaoka, 1980; Wourms and Evans, 1974
Cryptacanthodidae	3	4	North Atlantic, Pacific	3	3	2	Hart, 1973; Matarese, unpubl., Shiogaki, 1982
Pholidae	4	13	North Atlantic, Pacific	3	5	3	Breder and Rosen, 1966; Marliave, 1975; Rass, 1949; Sawyer, 1967; Tokuya and Amaoka, 1980
Anarhichadidae	2	6	North Atlantic, Pacific	2	3	2	Andriyashev, 1954; Barsukov, 1959; Breder, 1941; Kobayashi, 1961a; Marliave, 1975; Rass, 1949
Ptilichthyidae	1	1	Northeast Pacific	1	1	1	Kobayashi, 1961b; Richardson and Denhart, 1975
Zaproridae	1	1	Northeast Pacific	1	1	1	Chapman and Townsend, 1938; Haryu and Nishiyama, 1981
Scytalinidae	1	1	Northeast Pacific	0	0		

ous or large (Blenniini and Omobranchini) or completely lacking (Nemophini). Teeth develop early in most species; these become large (Nemophini) or hooked (Salariini) (Fig. 302E). Cirri may develop at the end of the larval period. Members of the Salariini have elongate pectoral fins (Fig. 302F).

Larvae of the northern families have an elongate body shape, but they range from moderately elongate (Zaproridae) to extremely long and thin (Ptilichthyidae) (Fig. 303). Heads are small, and initially pointed or rounded but become more pointed with development. Most species have a short to moderate snout. Preanal length is highly variable. Generally, preanal length is at least 50% BL, but it ranges from short (<50% BL in pre-

TABLE 144. SUMMARY OF EGG CHARACTERS IN BLENNIOIDEA. Blanks indicate data are unavailable.

Taxon	Egg type[1]	Single or mass	Egg diameter (mm)	Number of oil globules	Attachment processes or ornamentation	Pigmentation	Incubation (days)	Primary sources
Blennioidea								
Dactyloscopidae	D							Dawson, 1982
Xenocephalidae								
Notograptidae								
Tripterygiidae	D	Mass	0.90–1.40	Few to numerous	Filaments at one pole or everywhere	Embryo, yolk with "pigment spheres"	16–22	Graham, 1939; Miller et al., 1979; Ruck, 1973a; Ruck, 1980; Shiogaki and Dotsu, 1973
Clinidae	D[2]		0.96–1.7	Several	Filaments		12–40	Barnhart, 1932; Padoa, 1956h; Shiogaki and Dotsu, 1972b; Sparta, 1948; Stevens, unpubl.
Chaenopsidae	D							Stephens et al., 1966
Labrisomidae	D	Mass	1.15–1.33	1–6	Attach to each other, strands	Embryo, yolk	10	Breder, 1939
Blenniidae	D	Mass	0.58–1.6 × 0.4–0.96	0–several	Adhesive disk or pedestal	Embryo, yolk	6–61[3]	Cipria, 1934, 1936; Dotsu, 1982; Dotsu and Moriuchi, 1980; Dotsu and Oota, 1973; Dutt and Rao, 1960; Eggert, 1932; Fishelson 1963, 1976; Fritzsche, 1978; Hildebrand and Cable, 1938; Lebour, 1927; Mito, 1954; Munro, 1955; Peters, 1981; Qasim, 1956; Rao, 1970; Stevens and Moser, 1982; Thomson and Bennett, 1953; Watson, unpubl.; Wickler, 1957
Bathymasteridae	D	Mass	0.99–1.1	1	Non-adhesive mass		13–15	Breder and Rosen, 1966; Fitch and Lavenberg, 1975; Matarese, unpubl.
Stichaeidae	D	Mass	1.37–2.5	1	Adhesive		21	Breder and Rosen, 1966; Hart, 1973; Marliave, 1975; Matarese, unpubl.; Peppar, 1965; Shiogaki, 1983; Wourms and Evans, 1974
Cryptacanthodidae	D		1.8					Hart, 1973
Pholidae	D	Mass	1.4–3.0	1	Adhesive		42–70	Breder and Rosen, 1966; Marliave, 1975; Matarese, unpubl.; Sawyer, 1967
Anarhichadidae	D	Loose or clumps	4.0–8.0	1				Barsukov, 1959; Breder and Rosen, 1966; Matarese, unpubl.
Ptilichthyidae								
Zaproridae								
Scytalinidae								

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[1] D = demersal

[2] Ophiclini-ovoviparous George and Springer (1980). Clinini-viviparous (Penrith, 1969; Hoese, 1976)

[3] Usually 7–14 days.

TABLE 145. SUMMARY OF LARVAL SIZE AT SELECTED DEVELOPMENTAL STAGES IN BLENNIOIDEA (MM SL). Blanks indicate data are unavailable.

Taxon	Hatching	Notochord flexion	Special prejuvenile	Juvenile
Blennioidea				
Dactyloscopidae				
Xenocephalidae				
Notograptidae				
Tripterygiidae	2.7–6.1	4.8–<9.4	None	≥11.0
Clinidae	5.5–6.7	by 11.4–14.3	None	>16–25
Chaenopsidae				>16–17
Labrisomidae	4.1	4.9–6.9	None	>19–25
Blenniidae	2.0–5.4	3.6–10.75	4.6–26.0 Salariini	6.4–26.0
Bathymasteridae	5.5–6.0	<10.0	None	ca. 40.0
Stichaeidae	6.5–12.5 (8–9.5)	12.0–20.0 (13–15)	None	>25.0
Cryptacanthodidae	10.0–11.0	<18.0	Neustonic	ca. 30.0
Pholidae	10.0–12.5	ca. 19.0–30.0	None	>30.0
Anarhichadidae	17.0–18.0	<20.0	None	ca. 40.0
Ptilichthyidae	<20.0		None	ca. 114.0
Zaproridae	<12.0	<17.0	Neustonic	
Scytalinidae				

flexion Stichaeidae) to very long (Pholidae) (Fig. 303B, D). The family Anarhichadidae includes one genus with a long, thin bodied larva (*Anarrhichthys*) and another with only a moderately elongate larva (*Anarhichas*) (Fig. 303E). The monotypic family Ptilichthyidae has a unique larval form—it is highly elongate with a small head and extended postanal body (Fig. 303F).

Pigmentation characters.—Pigmentation is typically sparse for most families within this infraorder, and tends to be added subcutaneously with development. However, four families [Zaproridae, Anarhichadidae, Cryptacanthodidae, and some Nemophini (Blenniidae)] have larvae with dense body pigment that is not typical of the Blennioidea (Figs. 303C, E, and G). Important pigment areas are along the ventral body midline and in the gut area (Table 146).

Head.—Eyes are pigmented prior to hatching in all known groups. Pigment is generally absent or light during notochord flexion but usually increases dorsally, over the brain, by the time flexion occurs. Additionally, postflexion larvae may have pigment on the snout, mouth, and in the opercular area.

Gut.—Preflexion larvae in most species have peritoneal and some dorsolateral pigment. In families that have a gas bladder (e.g., Tripterygiidae, Labrisomidae, and Blenniidae), pigment is present on its dorsal surface (Fig. 302A, D). Ventral pigment may or may not be present. During notochord flexion, pigment increases on the lateral gut surface, and becomes subcutaneous in postflexion larvae.

Trunk and tail.—This is the most important pigment area for

TABLE 146. SUMMARY OF SOME PIGMENTATION CHARACTERS IN LARVAE OF BLENNIOIDEA. Key: D, dorsal; A, anal; P, pectoral; V, ventral; C, caudal; +, present; ○, absent; An, anterior; Po, posterior; ↑, increasing; ↓, decreasing; →, with development; and ○ → +, unpigmented initially, becoming pigmented with development.

	Head							Gut			
Taxon	Eye at hatching	Brain	Jaw	Snout	Opercle	Isthmus	Nape	Anterior	Dorsal	Ventral	Lateral
Tripterygiidae	+	+	○	○	○	○	○	○	+	○, +Po	○
Clinidae	+	○	○	○	○	○	○ → +	○	+	+Po	○
Chaenopsidae		○	○	○	○	○	○	○	○	○	○
Labrisomidae		○	○	○	○	○	○	○	+	+	○
Blenniidae	+	○, + → ↑	○	○	○	○	○	○	+ ↑	○ → + ↑	+ → ↑
Bathymasteridae	+	○ → +	○	○	○	+	○	○	+	+	○
Stichaeidae	+	○, +	○, +	○	○	+	○	○	+ → ↓	+	○
Cryptacanthodidae	+	+ ↑	+	+	+ ↑	○ → +	+	○	+ → ↓	○	○
Pholidae	+	○ → ↑	○	○	○	+	○	○	+	+	○
Anarhichadidae	+	+ ↑	+	+	+ ↑	+	○ → +	○	+ ↑	○ → +	+ → ↑
Ptilichthyidae		+	+	○	○	+	○	+	+	+	○ → +An
Zaproridae	+	+ ↑	+	+	+ ↑	+	+	○	+	○	+ ↑

identifying specific groups within this infraorder. Except for the densely pigmented families listed above, pigment along the dorsal body midline is rare in preflexion larvae. With development, pigment may increase along the dorsal midline or on the nape. Initially, lateral pigment is either absent or consists of a few spots internally along the notochord. After notochord flexion, internal and external pigment can increase ventrolaterally, or above and below the notochord (Stichaeidae, Bathymasteridae, and Pholidae). Typically, a series of ventral midline melanophores occurs in preflexion larvae. Although these melanophores may be absent in some families (Chaenopsidae, some Tripterygiidae), a number of families have larvae with up to 50 melanophores here (e.g., Blenniidae). The number, size, and shape of these melanophores can be very important when identifying groups. These spots may change shape with development (becoming y-shaped in Tripterygiidae and some Blenniidae), decrease in number (some Blenniidae and Stichaeidae), or become subcutaneous (Stichaeidae).

Fins.—With the exception of zaprorids and some blenniids, fins are rarely pigmented in preflexion larvae. After notochord flexion pigment develops on the various fins of blenniids, anarhichadids, and ptilichthyids (Table 146).

Hypural margin.—Pigment in the caudal area is usually lacking in preflexion larvae, and in postflexion larvae its presence is limited to a few families (Table 146).

Meristic characters.—The number of dorsal fins varies from one to three and in most families some combination of spines and rays is present, with spines predominating. Tripterygiids, clinids, and labrisomids may have up to three dorsal fins, the first two composed of spines. The total number of dorsal elements is highly variable but in some groups (stichaeids, anarhichadids, and ptilichthyids) well over 100 elements are present. The anal fin in most groups may include 1–2 spines. Stichaeids may have up to 5 anal spines. Information on the caudal fin is incomplete. In addition, from data available in the literature, principal rays and branched rays are not consistently distinguished. Most groups have between 9 and 15 (usually about 12–13) principal caudal fin rays and about 25–30 total caudal fin rays. All possess a pectoral fin with as few as 3 (labrisomids and clinids) or as many as 25 (zaprorids) fin rays. Pelvic fins can be present or absent. The northern families, except some stichaeids and pholids, lack pelvic fins. Tropical families usually possess thoracic pelvic fins with 1 spine and fewer than 5 rays (mostly 2–3 soft rays).

Vertebral counts are unknown for many blennioids or are based on few specimens. The number of vertebrae is highly variable within some families (e.g., stichaeids, blenniids, anarchichadids). In general, tropical families have a lower vertebral count than do northern families.

The order of fin ray development is highly variable in the Blennioidea. Information available on this is also inadequate, since in most studies reviewed here larvae have not been cleared and stained to determine the onset of ossification. In the tropical families where notochord flexion occurs as early as 3.6 mm, fin ray development may begin as early as 2.5 mm. Caudal fin rays develop first in clinid and labrisomid larvae, followed by the remaining fin rays soon after notochord flexion is complete. Typically, pectoral fin rays develop first in blenniid larvae (Blenniini and Salariini). In Ombranchini larvae (Blenniidae), the pectoral fin rays and caudal fin rays develop simultaneously. Among the northern families, data are insufficient to allow any generalizations. Fin rays begin forming at 9–15 mm in stichaeid larvae (usually caudal fin rays first) but may not be complete until larvae are 30 mm (Fig. 303B). Zaprorid and cryptacanthodid larvae begin caudal ray development about the time notochord flexion occurs. Fin ray development in ptilichthyid larvae begins with the dorsals and second anal at 40 mm.

RELATIONSHIPS

Although the scope of the available egg and larval data within the Blennioidea is limited, early life history characters reviewed here do not support the cohesiveness of this group. Due to a lack of unifying characters, the infraorder Blennioidea, as presently arranged, probably does not form a monophyletic group. Early life history characters appear to be more useful in clarifying relationships between families or within families rather than

TABLE 146. EXTENDED.

Trunk								
Dorsal margin	Dorso-lateral	Medio-lateral	Ventro-lateral	Ventral margin	Internal noto-chord	Hypural margin	Fin base	Diagnostic
+Po	○ → +	○	○	+	○	○	P	Anus, ventral midline
+ → ↑	○ → +	+ ↑	○	+	+	○	○	Gut, ventral midline
○	○	○	○	○	○	○	○	Lack of pigment
○, +Po	○	○	○	+	○	○	○	Swimbladder, ventral midline
○ → + An	○ → +	○ → + ↑	○ → ○, +	+ → ↓	+	○ → ○, +	○ → PV	Gut, ventral midline
○ → +	○	○	○ → +	+	+	○, +	○	Urostyle or lateral cross-checking
○ → +	○	+ → ↑	○ → +	+ → ↓	+	○ → ○, +	○	Gut, anus, ventral midline
+ ↑	+ ↑	+	+ ↑	+	–	○	○	Dense body
○ → ○, +	○	+	○	+	+	○ → ○, +	○	Gut, ventral midline
+ ↑	+ ↑	+ ↑	+ ↑	+	+	○	○ → DA	Dense body, fins
+	○	○	○	+ ↑	○	○	AP ○ → C	Gut, dorsal and ventral margin, caudal fin
+ ↑	+ ↑	+ ↑	+ ↑	+ ↑	–	+ ↑	AP → ↑ D	Dense body

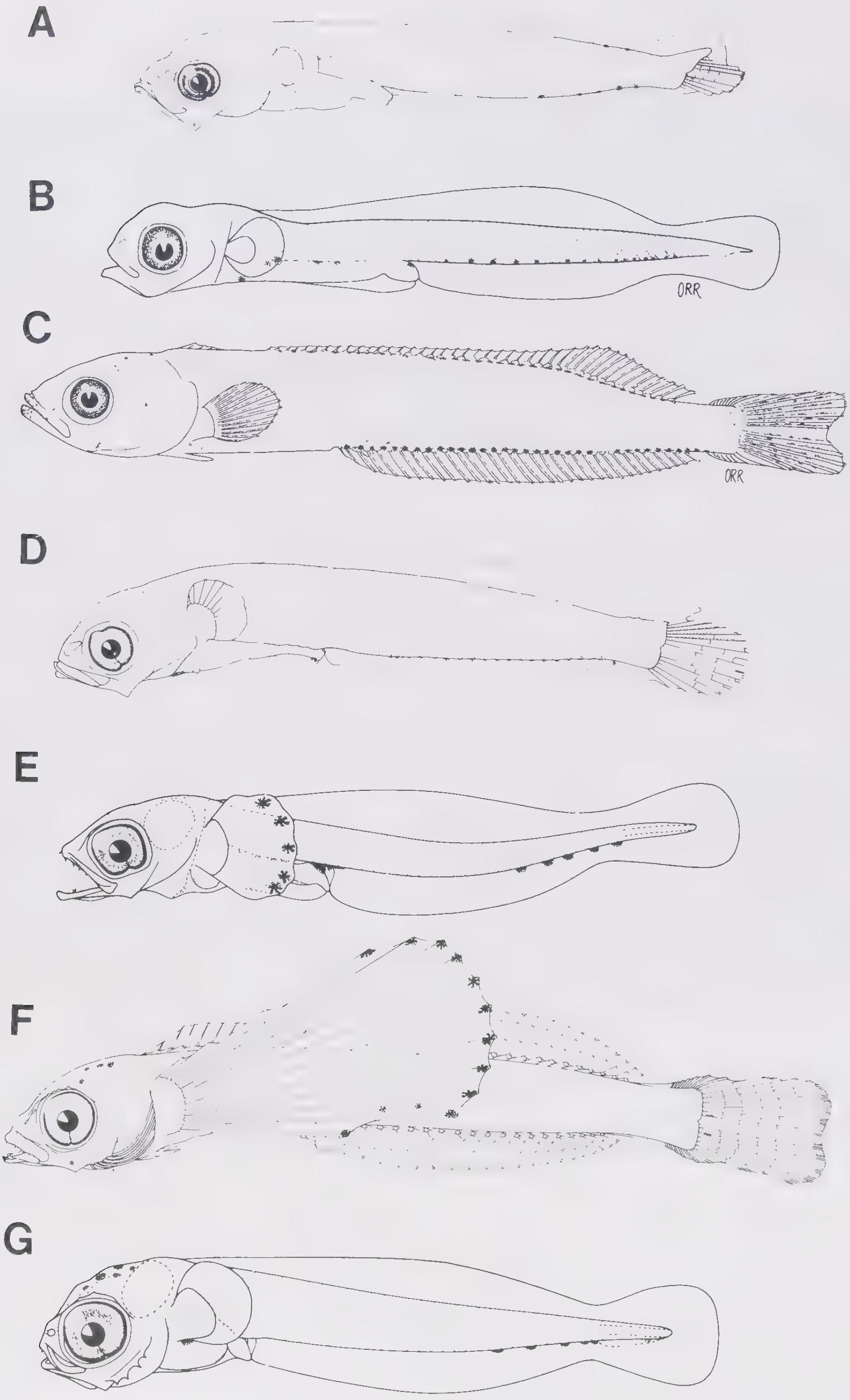

Fig. 302. Blennioidea larvae (tropical forms): (A) *Enneapterygius atriceps* (Tripterygiidae), 5.8 mm (from Miller et al., 1979 described as *Tripterygion atriceps*); (B–C) *Heterostichus rostratus* (Clinidae), 6.5 mm, 21.2 mm; (D) *Paraclinus integripinnis* (Labrisomidae), 7.2 mm; (E–F) *Istiblennius zebra* (Blenniidae), 3.3 mm, 11.0 mm (from Miller et al., 1979); (G) *Enchelyurus brunneolus* (Blenniidae), 3.2 mm (from Miller et al., 1979).

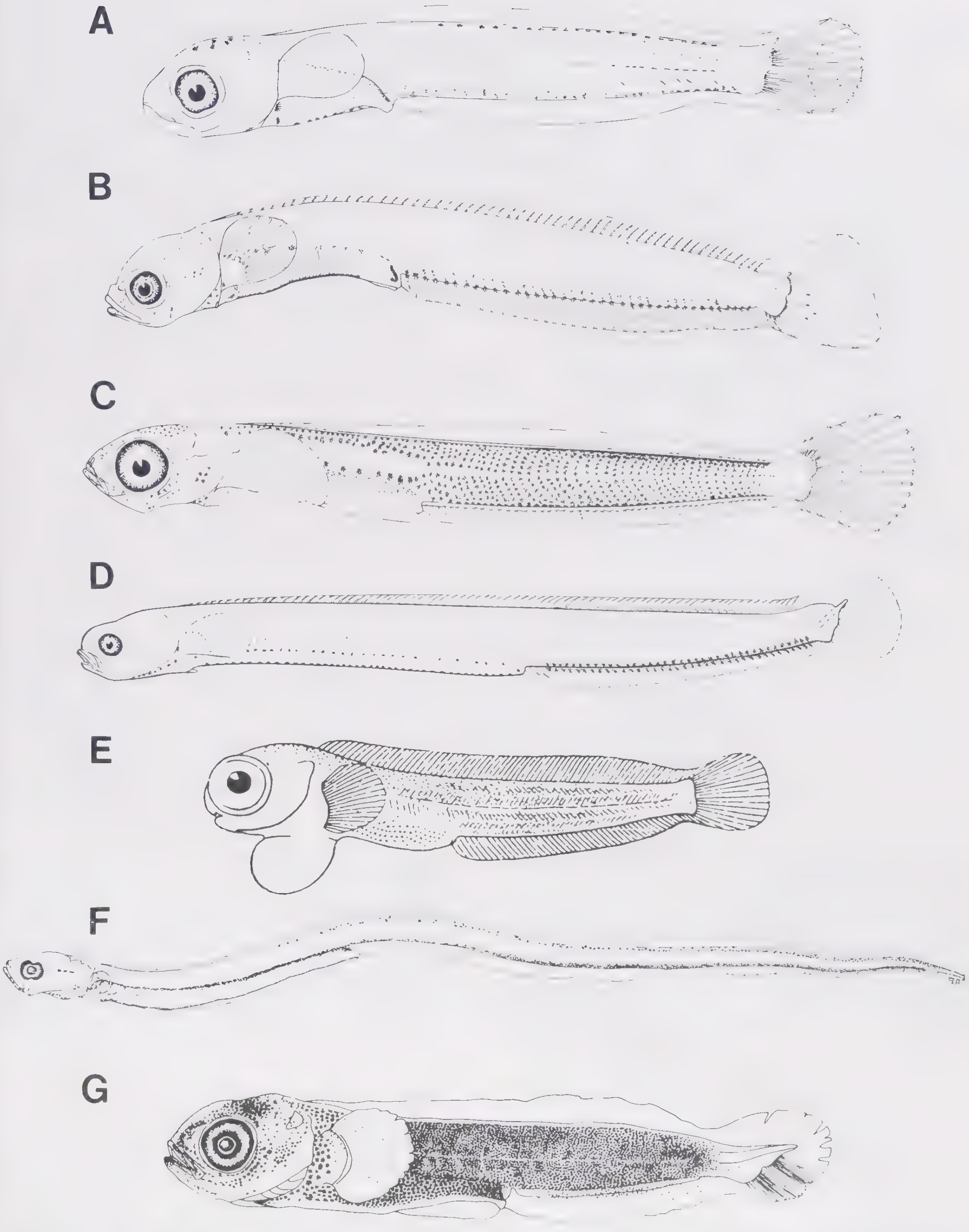

Fig. 303. Blennioidea larvae (northern forms): (A) *Ronquilus jordani* (Bathymasteridae), 10.4 mm; (B) *Anoplarchus purpurescens* (Stichaeidae), 12.0 mm, (C) *Lyconectes aleutensis* (Cryptacanthodidae), 16.0 mm; (D) *Pholis* sp. (Pholidae), 23.0 mm, (E) *Anarhichas lupus lupus* (Anarhichadidae), 24.5 mm (from Barsukov, 1959); (F) *Ptilichthys goodei* (Ptilichthyidae), 24.7 mm (from Richardson and Dehart, 1975), (G) *Zaprora silenus* (Zaproridae), 16.0 mm (from Haryu and Nishiyama, 1981).

Table 147. Summary of Selected Meristics in Blennioidea. Blanks indicate data are unavailable.

	Fins					
	Dorsal		Anal		Pectoral	Pelvic
Taxon	Spines	Rays	Spines	Rays		
Blennioidea						
Dactyloscopidae	0–VII + V–XVIII	14–36	II	22–41	12–16	I, 3
Xenocephalidae	—	7	—	10	21	5
Notograptidae						I
Tripterygiidae	III–VII + X–XXIV	7–15	0–II	14–30	10–19	I, 2–3
Clinidae	III + XXIV–LXXXIV	1–14	II	14–62	3–18	I, 2–3
Chaenopsidae	XVII–XXXIII	10–34	II	18–38	12–14	I, 3
Labrisomidae	III + I–IV + XX–LII	7–14	I–II	15–28	3–17	0–I, 0–3
Blenniidae	III–XVII	9–119	II	10–119	10–18	I, 2–4
Bathymasteridae	II	39–49	I–II	27–36	17–21	I, 5
Stichaeidae	XXII–CXXI	0–43	I–V	24–95	8–21	Absent or I, 1–5
Cryptacanthodidae	LX–LXXVII	—	II	45–50	11–15	Absent
Pholidae	LXXIV–CCL	—	I–II	29–53	10–16	Absent or I, 0–1
Anarhichadidae	LXX–CCL	—	0–I	42–233	18–23	Absent
Ptilichthyidae	LXXXIII–XC	115–148	—	179–196	13	Absent
Zaproridae	LIV–LVII	—	—	24–30	20–25	Absent
Scytalinidae		41–51	—	41–51	8	Absent

between Blennioidei infraorders, e.g., the similarity between labrisomid and clinid larvae and the differences between larvae in the various blenniid tribes.

Many of the families in Blennioidea include a large number of intertidal forms and many of the similarities (e.g., demersal eggs, parental care, and advanced state of newly hatched larvae) may be related to environmental conditions rather than to a close phylogenetic relationship. Additional study on the complete life history of these fishes is needed to identify unifying characters, if any exist. Studies at the family level will improve our knowledge of this unsatisfactorily defined group and facilitate outgroup comparisons.

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TABLE 147. EXTENDED.

Fins	Vertebrae			
Principal caudal	Precaudal	Caudal	Total	Primary sources
9–11	11–14	25–41		Böhlke and Caldwell, 1961; Böhlke and Chaplin, 1968; Dawson, 1974a, 1975, 1976, 1982; Kanazawa, 1952; Miller and Briggs, 1962; Myers and Wade, 1946
				Munro, 1967; Nelson, 1976
				Nelson, 1976
13–15	10–13	20–30	40–50	Bath, 1973; Leis and Rennis, 1983; Rosenblatt, 1959, 1960; Wheeler and Dunn, 1975
10–15	13–35	25–63		Böhlke, 1960b; George and Springer, 1980; Hoese, 1976; C. Hubbs, 1952, 1953a; Penrith, 1969; Scott, 1955, 1962, 1966, 1967; Shen, 1971; Springer, 1955, 1970; Stevens and Springer, 1974
13, 19–23			39–57	Böhlke, 1957; Greenfield, 1972; Johnson and Greenfield, 1976; Robins and Randall, 1965; Rosenblatt and Stevens, 1978; Smith-Vaniz and Palacio, 1974; Stephens, 1963, 1970; Stephens et al., 1966
10–14	10–14	20–33		Böhlke and Robins, 1974; Böhlke and Springer, 1961, 1975; C. Hubbs, 1952, 1953b; Rosenblatt and Parr, 1969; Rosenblatt and Taylor, 1971; Smith, 1957; Springer, 1954, 1955, 1958, 1959; Springer and Gomon, 1975b
10–15	9–16	19–119	28–135	Bath, 1976, 1978; Smith-Vaniz, 1975, 1976; Smith-Vaniz and Springer, 1971; Springer, 1967, 1968, 1971, 1972a, 1972b, 1976; Springer and Gomon, 1975a; Springer and Smith-Vaniz, 1972; Springer and Spreitzer, 1978; Stephens, 1970
14	14–16	35–39	49–54	NWAFC, unpubl.
3–8 + 3–9	14–43	29–72	46–113	Makushok, 1958; NWAFC, unpubl.; Shiogaki, 1980, 1981
13–15, 14	24–27	47–51	72–78	NWAFC, unpubl.; Shiogaki, 1982
6–7 + 6–7			80–107	Makushok, 1958; NWAFC, unpubl.
7–8 + 19–26	24–39	46–214	72–250	Barsukov, 1959; Makushok, 1958; NWAFC, unpubl.
	53–59	170–181	227–240	Makushok, 1958
30–31	24–26		61–62	Chapman and Townsend, 1938; NWAFC, unpubl.
				NWAFC, unpubl.

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Synopsis of Biological Data on Skipjack Tuna, *Katsuwonus pelamis*

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ABSTRACT

This synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*, includes information on nomenclature, taxonomy, morphology, distribution, reproduction, nutrition, growth, behavior, physiology, population structure, exploitation, and management of the species. Over 600 of the more important published and unpublished reports up to 1980, including some published in 1981, were consulted.

INTRODUCTION

There has been a major expansion in the world's skipjack tuna, *Katsuwonus pelamis*, fisheries in the past decade or so with the catch increasing better than twofold, from 320,000 metric tons (t) in 1969 to 699,000 t in 1979. While catches increased in both the Atlantic and Pacific Oceans, the most striking increase has been in the western central Pacific, which includes the Japanese southern water fishery and the fisheries of Papua New Guinea and the Solomon Islands. In this area the catches have risen over sevenfold, from 41,500 t in 1969 to 316,000 t in 1979.

The catch of skipjack tuna can probably be increased over present levels, but by how much is uncertain. To deal with the rational utilization of this resource as it approaches the level of full exploitation, it is imperative to have in hand all information concerning the biology, physiology, and various other factors relating to the fish and fishery.

Synopses of biological and technical data and information on the skipjack tuna by oceans were first compiled by Waldron (1963) for the Pacific Ocean, Postel (1963) for the Atlantic Ocean and Mediterranean Sea, and Jones and Silas (1963) for the Indian Ocean, and were presented at the Food and Agriculture Organization of the United Nations (FAO)-sponsored World Scientific Meeting on the Biology of Tunas and Related Species, 2-14 July 1962, at La Jolla, Calif. Forsbergh (1980) completed a synopsis of the species for the Pacific Ocean.

This paper reports current knowledge of the species in all oceans and reviews and evaluates, wherever appropriate, the results of past and recent research on the skipjack tuna through 1980.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Katsuwonus pelamis (Linnaeus 1758)

1.12 Objective synonymy

Scomber pelamis Linnaeus 1758 (original description); Osbeck 1765; Bonnaterre 1788; Gmelin 1788; Rafinesque 1810

Scomber pelamys Bloch and Schneider 1801; Risso 1810; Cuvier 1829; Valenciennes 1836

Scomber pelamides Lacépède 1802

Thynnus pelamis. Risso 1826; Steindachner 1868; Hoek 1904

Thynnus vagans Lesson 1828 (original description), 1830

Thynnus pelamys. Cuvier and Valenciennes 1831; Temminck and Schlegel 1842; Cantor 1850; Bleeker 1856; Günther 1860, 1876; Playfair and Günther 1866; Day 1878; Lütken 1880; Macleay 1881; Eigenmann and Eigenmann 1891; Richard 1905; Cunningham 1910; Parona 1919

Pelamys pelamys. Bleeker 1862, 1865

Orcynnus pelamys. Poey 1868; Goode and Bean 1879; Goode 1884

Euthynnus pelamys. Jordan and Gilbert 1882; Carus 1893; Joubin and Le Danois 1924

Gymnosarda pelamis. Dresslar and Fesler 1889; Jordan and Evermann 1898; Jenkins 1904; Snodgrass and Heller 1905; Evermann and Seale 1907; Jordan 1907; de Miranda Ribeiro 1915; Meek and Hildebrand 1923; Breder 1929; Hornell 1935; Palma 1941

Euthynnus pelamis. Smitt 1893; Starks 1910; Tanaka 1912; Jordan and Jordan 1922; Bigelow and Welch 1925; Fowler 1928, 1938; Herre 1932; Deraniyagala 1933; Nobre 1935; Smith 1949; de Beaufort and Chapman 1951; Bigelow and Schroeder 1953; Steinitz and Ben-Tuvia 1955; Fourmanoir 1957; Bailey et al. 1960, 1970; Collette and Gibbs 1963; I. Nakamura 1965; Robins et al. 1980

Katsuwonus pelamys. Kishinouye 1915; Frade and de Buen 1932; Le Gall 1934; Morrow 1957

Gymnosarda pelamys. Thompson 1918; Barnard 1925

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Katsuwonus pelamis. Kishinouye 1923; de Buen 1926, 1930, 1935, 1958; Jordan et al. 1930; Soldatov and Lindberg 1930; Ehrenbaum 1936; Seale 1940; Serventy 1941; Godsil and Byers 1944; Nichols and Murphy 1944; Fowler 1945; LaMonte 1945; Clemens and Wilby 1946; Hildebrand 1946; Brock 1949; Rivas 1949, 1951; Herre 1953; Belloc 1955; Munro 1955, 1958; Briggs 1960; Jones and Silas 1960, 1963, 1964; Schultz 1960; Postel 1963, 1964; Talbot 1964; Whitley 1964; Williams 1964; Collette 1978

Katsuwonus vagans. Jordan et al. 1930; Barnhart 1936; Okada and Matsubara 1938; Fowler 1949

Katsuwonis pelamis. Herre 1933 [typographical error?]

Euthynnus (*Katsuwonus*) *pelamis*. Fraser-Brunner 1950; Mendis 1954; Bini and Tortonese 1955; Williams 1956; Scaccini et al. 1975

1.2 Taxonomy

1.21 Affinities

Phylum Vertebrata
  Subphylum Craniata
    Superclass Gnathostomata
      Series Pisces
        Class Teleostomi
          Subclass Actinopterygii
            Order Perciformes
              Suborder Scombroidei
                Family Scombridae
                  Subfamily Scombrinae
                    Tribe Thunnini
                      Genus *Katsuwonus*
                        Species *pelamis*

The Family Scombridae was defined by Regan (1909) and further clarified by Starks (1910), who divided it into five subfamilies: Scombrinae, Scomberomorinae, Acanthocybinae, Sardinae, and Thunninae. Kishinouye (1915) divided Regan's Scombridae into three Families: Scombridae, Cybiidae, and Thunnidae. He subsequently (1917) split Thunnidae into two Families, Thunnidae and Katsuwonidae, and placed both into a newly erected Order Plecostei on the basis of their well-developed subcutaneous vascular system. Takahashi (1924), however, rejected Kishinouye's new order, pointing out that the subcutaneous vascular system was not unique to tunas, but was also found in swordfish, *Xiphias gladius*; dolphin, *Coryphaena hippurus*; stargazer, *Gnathagus elongatus*; goby, *Aprocryptes chinensis*; and puffer, *Sphoeroides rubriceps*. These two views have persisted to the present.

Berg (1940) followed Kishinouye in placing the tunas into a single Family Thunnidae and renamed the Order Thunniformes. He relegated Katsuwonidae to subfamily status as Auxidini. Some investigators retained the Family Thunnidae, while relegating Katsuwonidae to generic status (Fowler 1945; Herre 1953; Morrow 1954, 1957; Munro 1955). Zharov (1967) divided the Thunnidae into two subfamilies, Thunninae and Katsuwoninae, while others recognized the Families Thunnidae and Katsuwonidae (Jordan and Hubbs 1925; Barnhart 1936; Kamohara 1941; Morice 1953; Godsil 1954).

Most other investigators followed Regan and Stark's classification, maintaining the Family Scombridae as a natural unit (Barnard 1925; Fowler 1928; Hildebrand 1946; Schultz and Stearn 1948; Smith 1949; Fraser-Brunner 1950; de Beaufort and Chapman 1951; Rivas 1951; Jones and Silas 1960, 1963, 1964; Schultz 1960; Collette and Gibbs 1963; Waldron 1963; I. Nakamura 1965; Gibbs and Collette 1967; Collette and Chao 1975; Collette 1978). Fraser-Brunner (1950) recognized only the subfamilies Gasterochismatinae and Scombrinae. I. Nakamura (1965) added a third subfamily, Thunninae, but Collette and Chao (1975) reverted to two subfamilies, as proposed by Fraser-Brunner, and split the Scombrinae into two tribes, placing Scombrini (the more primitive mackerels) and Scomberomorini (the Spanish mackerels) in one group and Sardini (the bonitos) and Thunnini in the other (Fig. 1).

Opinion on the generic name also has differed over the years and the differences continue to this day. Jordan and Gilbert (1882) credit Lütken for establishing the genus *Euthynnus* and separating *alliteratus* and *pelamys* from the other tunas largely on the basis of an important osteological character, the trellis formed on a portion of the abdominal vertebrae. Kishinouye (1915) established the genus *Katsuwonus* and separated it from *Euthynnus* based on differences in internal characters. Since then many others have recognized *Katsuwonus* (de Buen 1930; Jordan et al. 1930; Herre 1932; Serventy 1941; Godsil and Byers 1944; Clemens and Wilby 1946; Hildebrand 1946; Rivas 1951; Godsil 1954; Belloc 1955; Munro 1955; Briggs 1960; Gosline and Brock 1960; Jones and Silas 1960; Schultz 1960; Postel 1964; Talbot 1964; Whitley 1964; Zharov 1967; Collette and Chao 1975; Collette 1978).

Fraser-Brunner (1950), in his attempt to maintain the Family Scombridae as a natural unit, synonymized *Katsuwonus* with *Euthynnus*, as did other investigators (de Beaufort and Chapman 1951; Bigelow and Schroeder 1953; Mendis 1954; Bini and Tortonese 1955; Williams 1956; Bailey et al.

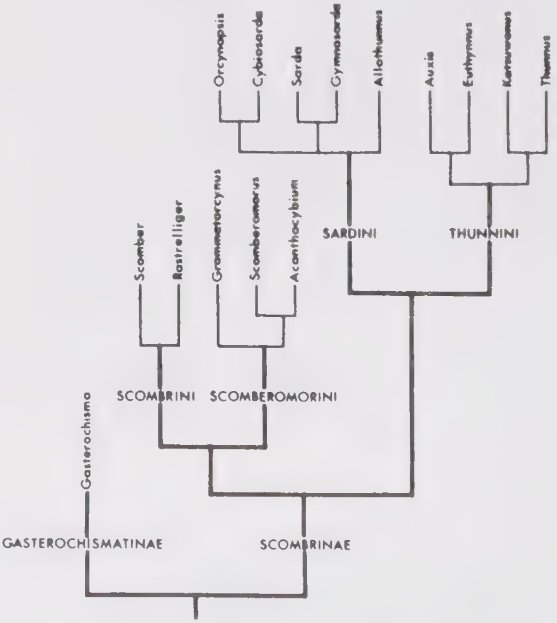

Figure 1.—The subfamilies, tribes, and genera of the Scombridae (from Collette and Chao 1975).

1960, 1970; Collette and Gibbs 1963; I. Nakamura 1965; Robins et al. 1980). Of those who relied heavily upon internal characters, I. Nakamura (1965) supported his choice on the basis that in both genera the atlas was not reduced in size and the alisphenoids did not meet ventrally at the median line. Robins et al. (1980), noting that the structure of the bony shelf that divides the anterior six vertebrae into dorsal and ventral portions is shared by *Auxis*, *Euthynnus*, and *Katsuwonus* only, suggested that the latter was more intimately related to *Euthynnus* than to *Thunnus*.

Because of the close relationship of these two genera, similarities in a number of characters such as noted above, are expected; however, the differences pointed out by Kishinouye (1923), Godsil and Byers (1944), Godsil (1954), and Collette (1978) seem large enough to justify their separation. These differences include the following:

1) The dorsal and ventral branches of the cutaneous artery in *Katsuwonus* are about equally developed, instead of having the ventral branch short and dendritic as in *Euthynnus*.
2) The trellis on the vertebral column moves the aorta ventrally a distance slightly less than the depth of a centrum in *Katsuwonus*; less than in *Auxis* and *Euthynnus*, but more than in *Thunnus*.
3) The liver in *Katsuwonus* resembles that of the yellowfin group of *Thunnus* more than *Euthynnus* and *Auxis* because the right lobe does not extend the length of the body cavity.
4) Hepatic veins are absent from the ventral surface of the liver in *Katsuwonus*, as opposed to *Auxis* and *Euthynnus*.
5) The prefontals are smaller in *Katsuwonus* and do not project into the dorsal outline in dorsal view.
6) The edge of the posterior orifice of the myodome in *Katsuwonus* is nearly vertical, whereas it is roughly spherical in *Euthynnus*.
7) The exoccipital condyle in *Euthynnus* projects beyond the transverse margin of the skull a distance approximately equal to the length of the first vertebra, whereas it is much shorter in *Katsuwonus* and equals roughly half the length of the first vertebra.
8) *Katsuwonus* has 41 vertebrae, whereas *Euthynnus* has 39 or fewer.

Attempts to determine generic relationships between *Katsuwonus* and *Euthynnus* by serological and immunogenetic techniques have also given mixed results. Electrophoretic analyses of hemoglobin (Sharp 1969, 1973) have indicated that *Katsuwonus* differs from *Euthynnus* and *Thunnus*. *Katsuwonus* has only two hemoglobin bands; *E. alletteratus* and *E. affinis* have three identical bands; and the four species of *Thunnus* examined (*albacares*, *alalunga*, *sibi*, and *thynnus*) have at least four bands. One of the bands in *Katsuwonus* and *Euthynnus* seems to be identical whereas none of the hemoglobins in *Katsuwonus* or *Euthynnus* is identical to any hemoglobin in the four species of *Thunnus* examined. Analyses of heart, red and white muscle tissues, and enzymes, on the other hand, have provided conflicting evidence. Sharp and Pirages (1978) found that *K. pelamis* and *E. affinis* were the most closely related of the non-*Thunnus* tunas, that both species were almost equally close to *T. albacares*, and that *E. lineatus* and *Auxis thazard* were about as close to each other as were *K. pelamis* to *E. affinis*, but somewhat more distantly related to *T. albacares*, and, therefore, to the *K. pelamis-E. affinis* group. The authors indicated that their results showed little reason for separating *Katsuwonus* from *Euthynnus*. While this seems to be true when considering only *E. affinis*, the distance between *affinis* and *lineatus* and the latter's close relationship with *A. thazard* suggests otherwise.

We thus agree with Collette's (1978) view that placing *Katsuwonus* in synonymy with *Euthynnus* would obscure the relationships of *Euthynnus* with *Auxis* and *Katsuwonus* with *Thunnus*.

1.22 Taxonomic status

The name *pelamis* was established by Linnaeus in 1758 and was accepted by workers throughout the remainder of the 18th century. Bloch and Schneider (1801) used the name *pelamys* and most workers also used this name in the 1800's and early 1900's. Some of these, notably Cuvier (1829), Valenciennes (1836), Temminck and Schlegel (1842), Cantor (1850), Bleeker (1856), and Günther (1860), although spelling the name *pelamys*, attributed the authorship to Linnaeus. Two other names, *pelamides* by Lacépède (1802) and *vagans* by Lesson (1828), were used briefly. Both names reflected differences in the geographic locality of capture. The name *pelamis* gained in acceptance between 1890 and 1935, and nearly all workers today use this name.

Existing morphological and meristic descriptions of the skipjack tuna, *Katsuwonus pelamis*, from all oceans (Jones and Silas 1963; Postel 1963; Waldron 1963) and biochemical genetic study by Fujino (1969) indicate that there is but one worldwide species—*Katsuwonus pelamis*.

1.23 Subspecies

No subspecies are recognized.

1.24 Standard common and vernacular names

The standard common and vernacular names of the skipjack tuna, obtained from various sources (Herre and Umali 1948; Rosa 1950; Herre 1953; Okada 1955; Van Pel 1960; Jones and Silas 1963; Postel 1963; Waldron 1963; Moreland 1967; Miyake and Hayasi 1972) are listed in Table 1.

1.3 Morphology

1.31 External morphology (and description)

Body robust, rounded in cross-section and full in outline; maxillary not concealed by preorbital; about 40 teeth on jaws, but absent on vomer and palatines; corselet is well defined with hardly any scales visible on rest of body; interspace between 1st and 2d dorsal fins hardly exceeding eye diameter; lateral line with a decided downward curve below 2d dorsal fin; margin of 1st dorsal fin strongly concave; pectoral fin short and triangular reaching posteriorly to the 9th or 10th dorsal spine most commonly, but to only the 8th or as far as the 11th spine in exceptional specimens (Fig. 2).

Table 1.—Common and vernacular names of skipjack tuna.

Country/locality	Standard common name	Vernacular name
Aden, Gulf of		AF muss; dabub; hargheiba
Albania	Palamida	
Angola	Bonito	
Australia	Striped tuna	Watermelon; skipjack
Brazil	Bonito de barriga listada	Bonito rajado
British Guiana	Oceanic bonito	White bonito
British West Indies	Oceanic bonito	White bonito; banjo; barriolet
Canada	Skipjack; thonine à ventre rayé	Skipjack tuna; oceanic bonito; striped bonito
Canary Is.	Bonito	
Chile	Atun	Cachurreta; cachureta; cachorreta; barrilete
Cuba	Atun	Merma
Denmark	Bugstribet bonit	
East Africa and Zanzibar	Skipjack	Sehewa (also refers to *Euthynnus* sp., *Auxis* spp.)
France	Listao; bonite; bonitou; bounicou	Bonite à ventre rayé
Germany	Echter bonito	Bauchstreifiger
Greece	Pelamys	Pelamis; tonina
India	Oceanic skipjack	Bonito; kali-phila-mas; varichoora; choora; metti
Indonesia	Cakalang	Tjakalang; tjakalang-lelaki; tjakalang-perempuan; tjakalang-merah; skipjack
Israel	Balamida	
Italy	Palometta	Paamia; paamitun; palametto; palamida; palamatu; palamia; tonina de dalmazia; nzirru; palamitu impiriali; tonnetto
Japan	Katsuo	Katuwo, katsuwo; magatsuwo; mandagatsuwo; mandara; hongatsuo
Korea	Ga-da-raeng-i	Ga-da-ri; yeo-da-raeng-i; gang-go-deung-so; so-young-chi; mog-maen-dung-i; da-raeng-i
Madagascar	Bonite	Bonite à ventre rayé; diodary; m'bassi
Madeira Is.	Gaiado	
Maldives	Kadumas (small); Godhaa (large)	Skipjack tuna
Mexico	Barrilete	
Monaco	Bonita	
Morocco	Listao	L'bakoura
New Guinea	Tjakalang	
New Zealand	Bonito	Striped bonito; striped tunny; skipjack; skipper
Norway	Bonit	
Peru	Barrilete	
Philippine Is.	Gulyasan	Striped tuna; skipjack; pundahan; bankulis; sobad; oceanic bonito; bonito; palawayan; puyan; tulingan
Poland	Bonite	
Polynesia (except Tahiti and Hawaii)	Atu	Bonito
Portugal	—	Gaiado; bonito de ventre raiado; bonito; listado; gayado; sarrajao, serra
Roumania	Palamida	Palamida lacherda
Senegal	Kiri-kiri	
South Africa	Skipjack	Skipjack tuna; oceanic bonito; lesser tunny; bonito; watermelon; katunkel
Spain	Listado	Skipjack; atun de altura; bonito de veintre rayado; bonito; palomida; bonitol; bonito de altura; lampo; llampua; bonito del sur; bonita
Sri Lanka	Bonito	Balaya; scorai
Sweden	Bonit	
Tahiti	Auhopu	
Taiwan	Theng chien	
Tunisia	Boussenna	Bonite
Union of Soviet Socialist Republics	—	Okeanskii bonito; katsuo; polosatyi tunets
United Kingdom	Striped bellied bonito	Striped bellied tunny; bonito
United States of America	Skipjack tuna	Skipjack; arctic bonito; oceanic skipjack; striped tuna; watermelon; victor fish; striped bonito; oceanic bonito; skippy; ocean bonito; mushmouth; aku (Hawaii); aku kinai (Hawaii)
Yugoslavia	Trup prugavac	Tunj prugavac

Body color in life is steel blue, tinged with lustrous violet along the dorsal surface and decreasing in intensity on the sides to the level of the pectoral fin base; half of the body, including the abdomen, is whitish to pale yellow; evanescent vertical light bars are seen on the sides of the body immediately after capture; and a light grayish tinge on the underside of the mandible merges posteriorly with the whitish color on the lower half of the body. Four to six black longitudinal stripes are conspicuous below the lateral line on each side of the body. Matsumoto et al. (1969) described two specimens, one taken in Hawaiian waters, the other off Honduras, which lacked these stripes. They, however, represent extremely rare cases.

The counts of body parts for specimens from all oceans are given in Table 2. There seems to be no difference in the counts on fish from the Pacific and Indian Oceans and in at least two characters, first dorsal spines and gill rakers, on fish from all oceans.

Anatomical descriptions of the species may be found in Kishinouye (1923) and Godsil and Byers (1944). The vertebral column (Fig. 3) differs sufficiently from that of other fishes to be worthy of comment. Godsil and Byers (1944) wrote "The spinal column is extremely complex in this species. In the posterior half of the precaudal, and the anterior part of the caudal region, haemapophyses arise at both ends of each vertebra, with the anterior haemapophyses of one vertebra articulating with the posterior haemapophyses of the preceding vertebra. These haemapophyses project far below the spinal column and alternate with the longer haemal spines described below. An osseous bridge roughly parallel with the spinal column unites the anterior and posterior haemapophyses of each vertebra. Viewing the spinal column laterally, the bridge and the circular opening it forms may be easily seen. A branch arises from each bridge and extends downward to unite in the median line with its fellow from the opposite side. This forms the haemal arch from the tip of which a single haemal spine continues ventralward."

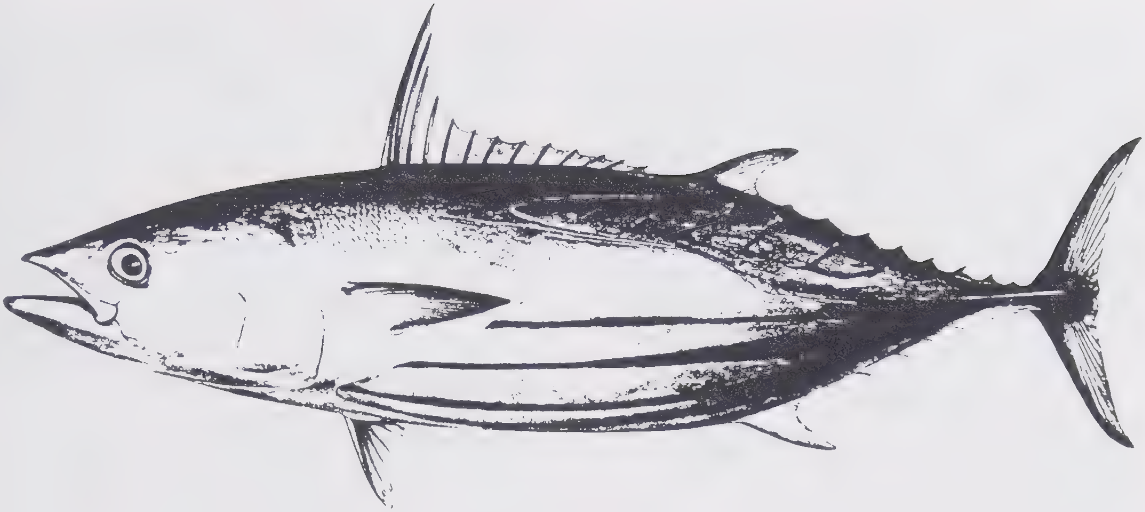

Figure 2.—The skipjack tuna, *Katsuwonus pelamis* (Linnaeus).

Table 2.—Counts of body parts for the skipjack tuna, *Katsuwonus pelamis*, from the Pacific, Indian, and Atlantic Oceans.

Characters	Pacific Ocean Japan, Hawaii, E. Pacific (Waldron 1963)	Indian Ocean E. Africa, Sri Lanka, Laccadive Is., Indonesia, Australia (Jones and Silas 1963)	Atlantic Ocean Cape Vert (Postel 1963)	All oceans	
					(Mostly
1st dorsal spine	14-17	14-17	14-16	14-17	15-16)
2d dorsal rays	13-16	13-16	—	13-16	(14-15)
Dorsal finlets	7-10	7-9	—	7-10	(8)
Anal rays	13-16	13-17	—	13-17	(14-15)
Anal finlets	7-8	7-8	—	7-8	(7)
Pectoral rays	24-32	26-30	—	24-32	(26-30)
Gill rakers					
Upper	18-22 +	18-21 +	—	18-22 +	(18-20)
Lower	35-43	33-42	—	33-43	(38-41)
Total	53-63	50-63	51-62	50-63	(56-60)

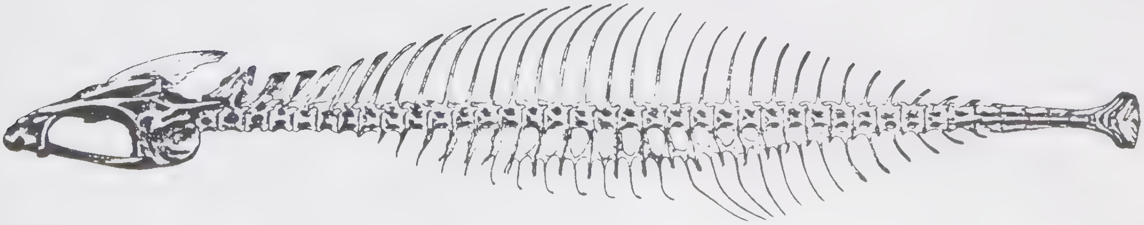

Figure 3.—Axial skeleton of an adult skipjack tuna (from Godsil and Byers 1944).

Such complex basketwork also occurs in the *Euthynnus* (Godsil 1954), but whereas the haemal arch in *K. pelamis* occurs adjacent to the vertebral column, that in *Euthynnus* is positioned away from the vertebral column (Fig. 4) at the tips of the haemapophyses. Viewing the vertebral column laterally, the inferior foramina in *Euthynnus* are elongate and about twice as long as those in *K. pelamis.*

The absence of consistent differences in both external and internal morphological characters of skipjack tuna from widely separated regions in the Pacific (Godsil and Byers 1944) indicates that there is but one species of skipjack tuna and that it is not possible to define subpopulations on the basis of these characters.

1.32 Cytomorphology

No information is available on chromosome number of skipjack tuna.

1.33 Protein specificity

The inability of standard morphometric analyses to resolve the problem of subpopulation or stock separation in skipjack tuna has led to the utilization of population genetic methodologies. Initial attempts involved the study of blood types through antigen-antibody reactions, and this was followed by some work on polymorphisms of the protein hemoglobin using starch-gel electrophoresis. As in other applications of population genetics, most work now involves the study of various serum and tissue enzymes, again using starch-gel electrophoresis. Sera are more commonly used because collecting the sample does not decrease the commercial value of the catch. Early isoenzyme studies involved samples collected from the central Pacific, then rather quickly from the eastern Pacific, Atlantic, western Pacific, and finally the Indian Ocean.

(1) Blood groups

Cushing (1956), who pioneered the application of blood typing for the study of tuna subpopulations, found two phenotypes on the basis of the agglutination of skipjack tuna erythrocytes in normal bovine serum. Subsequently, Sprague and Holloway (1962) named this system the C blood group apparently after Cushing. In the same paper, they published information on another blood group, B, and on blood factors A, D, and F which were not shown to belong to any inheritance system. Fujino (1967, 1969) found that the frequency of the K_1-positive phenotype of the B group was related to the size of skipjack tuna. Several papers were published after this purporting to have found or not to have found evidence of subpopulations from various areas in the Pacific Ocean (Sprague and Nakashima 1962; Sprague et al. 1963; Sprague 1963; Fujino 1969, 1970b, 1972). Neither the C nor B groups were shown to be amenable to Hardy-Weinberg analysis, and neither of these blood groups proved useful for population genetics studies.

Fujino and Kazama (1968) found another blood group, Y, which again did not prove useful in separating subpopulations, except when used together with other gene systems (Fujino 1969, 1970a). The Y group is made up of 15 phenotypes, coded by 6 codominant alleles; however, only 2 alleles, Y^y and Y^{so}, and the 3 resultant phenotypes are abundant enough to be useful in population studies. The system was shown to be amenable to Hardy-Weinberg analysis and independent of sex, size (age), and the C and B blood groups. Samples from various areas in the eastern, central, and western Pacific Ocean and the Atlantic Ocean failed to show heterogeneity of genotypic frequencies; however, the lower frequency of the Y^y allele found in the Atlantic Ocean indicates greater opportunity for divergence and, therefore, utility in subpopulation differentiation.

Fujino (1970a, 1971) described some preliminary results for an H blood group consisting of two phenotypes. While there was some evidence for the existence of subpopulations within the east-central Pacific Ocean (by testing phenotypes), the system was not shown to be amenable to Hardy-Weinberg analysis.

(2) Hemoglobins

Little work has been performed using hemoglobins because their instability requires preservation techniques that are hard to apply at sea and because they are not highly polymorphic.

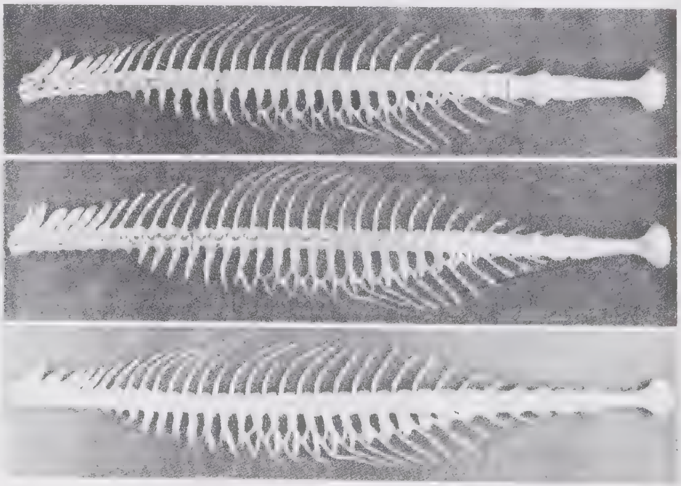

Figure 4.—Vertebral column of *Euthynnus.* Top to bottom: *lineatus, yaito* (= *affinis*), *alletteratus* (from Godsil 1954).

All samples examined by Sharp (1969, 1973) from off Baja California and Hawaii showed two phenotypic bands; therefore, the author made no inferences regarding subpopulation differentiation.

(3) Serum isoenzymes

While it is true that serum enzymes have provided the richest material for differentiating subpopulations of skipjack tuna, only esterase and transferrin, and recently guamine deaminase, have actually been found to be sufficiently polymorphic. In the mid-1960's while testing a series of tissues sampled from skipjack tuna collected off Hawaii, Sprague (1970) found six electrophoretic zones of esterases, one of which he interpreted as serum esterase. He hypothesized that the four observed phenotypes are coded by three alleles. Using blood serum, Fujino (1967) and Fujino and Kang (1968a) found three clear and three faint bands of serum esterase activity resulting in nine observed phenotypes and hypothesized, on the basis of the Hardy-Weinberg law, that they are coded by six codominant alleles. We follow the conventional allele numbering system based on relative mobility, hence the most abundant allele in the eastern and central Pacific is Est 2, rather than number 1 as in Fujino's papers (the reason for this difference is historical in that the now Est 1 is rare and was found after much work was already published). Because the faint bands are so rare, the system is usually treated as a six phenotype, three allele system for subpopulation study. The transferrin gene system was first described for skipjack tuna by Barrett and Tsuyuki (1967) from samples collected in the eastern tropical Pacific. They observed six phenotypes and hypothesized that they are coded by three codominant alleles. Researchers at the Australian National University (South Pacific Commission (SPC) 1981) have reportedly tested 42 gene loci (proteins) and found only 3 that were highly polymorphic. Glucose-phosphate isomerase, 6-phosphogluconate dehydrogenase (also reported by Sharp and Kane[3]), and apparently adenosine deaminase were variable but at low levels. Research on the esterase, transferrin, and guamine deaminase gene systems will be discussed in some detail below.

After the observed serum esterases were hypothesized to compose a single gene locus consisting of six codominant alleles, the locus was shown to be independent of sex, size, blood groups B, C, and Y, and serum transferrin (Fujino 1967, 1970a; Fujino and Kang 1968a, b). While these basic and essentially genetic factors were being established, the search for subpopulations, which was the real purpose of the studies, proceeded. Such population genetics studies involve testing individual sample lots for genetic equilibrium and testing for homogeneity both within and between sample lots from arbitrary areas. These tests are quite technical since they involve inheritance properties of the multinomial Hardy-Weinberg law, chi-square tests of homogeneity or, more recently, the *G*-test of Sokal and Rohlf (1969), and considerations of the effect of sample size on these tests. A great deal of controversy has surrounded the employment of these tests, i.e., the confidence to be placed on the results, and has led to three different approaches being followed by various scientists and organizations.

The first approach was advanced by Kazuo Fujino who was associated with the Honolulu Laboratory, National Marine Fisheries Service, and is now with the Kitasato University in Japan. Fujino (1970a) showed that the Hardy-Weinberg method is not very sensitive to deviations from expected proportions (genetic nonequilibrium) by employing a simple theoretical test. Taking the calculated allelic frequencies for the eastern-central and western subpopulations (to be described later) and constructing a one-to-one mixture of these subpopulations, lack of fit to Hardy-Weinberg proportions could not be shown with a sample size of 100 individuals (nor, we might add, would have been found if he had used a sample of 200 individuals). Later Fujino (1971) presented graphic evidence showing that a mixture of subpopulations could always be detected for a sample of 100 individuals from a one-to-one mixture of subpopulations having a difference > 0.443 in the frequency of the allele being tested, whereas a mixture could never be detected if the difference were < 0.328. For differences falling between 0.328 and 0.443, ability to detect a mixture depended on the absolute allelic frequencies. While an examination of the effect of sample size shows that it is, of course, easier to determine a mixture with larger sample sizes, Fujino's data indicate that the differences in the allelic frequencies between the hypothesized eastern-central and western subpopulations preclude the ability to consistently detect mixtures with a sample size of 100 (or as we said, even 200). From this result, Fujino seems to have concluded that a reasonable strategy would be to collect small samples (generally < 100 individuals) and to sample more schools. He has then proceeded to search for subpopulations by grouping sample lots (schools) from similar geographical areas, by testing for intra- and inter-area homogeneity, and by setting up statistical confidence regions for classifying individual school samples into separate subpopulations, without considering whether the individual schools represented mixtures of genetic units.

Fujino (1967) and Fujino and Kang (1968a) presented results from their initial examination of material from the Atlantic, Hawaiian Islands, the northeastern tropical Pacific, Palau Islands, and Japan. They found no evidence of heterogeneity of samples within these areas, nor between Hawaii and the eastern tropical Pacific or between Palau and Japan. However, their tests did show that samples from Hawaii were different from the combined samples from Palau and Japan; and Atlantic material was different from that collected in the eastern Pacific. Fujino (1969) used both the esterase system and the Y blood group in attempting to separate subpopulations. Using rejection ellipsoids for Y^y and Est 2, he found that the eastern-central Pacific samples overlapped with those from the western Pacific, and these, in turn, overlapped with samples from the Atlantic. Thus, while the Atlantic material was shown to be different from the eastern-central and western Pacific material, the employment of these two gene systems did not contribute to differentiating between eastern-central and western Pacific material. He also stated that there was no evidence of heterogeneity (for any of the five gene systems, including esterase and blood group Y) between the Caribbean Sea and Gulf of Guinea (three and five sample lots, respectively). Fujino (1970a) for the first time actually used the names eastern-central and western subpopulations and restated that he had found no evidence of heterogeneity of samples within these areas, even with the inclusion of new material such as those from Ecuador. Also for the first time, Fujino described the boundary between these two subpopulations, and he did this by assigning schools to either of the subpopulations based on rejection limits for Est 2. While the western subpopulation was shown to be present the entire year in inshore waters off the east coast of the main Japanese Islands and around the Ryukyu Islands, the Bonin-northern Mariana Islands chain, and Palau Islands, he stated that the boundary between the subpopulations shifts easterly in the summer and westerly in the fall and winter in the waters between the Bonin-northern Mariana chain and the international dateline. Then in the same year, Fujino (1970b) presented additional information on these subpopulations, namely, that there was no evidence for seasonal variation in the esterase gene frequency in either Hawaii or Palau, that new material from the Line Islands was not different from the historical Hawaiian material, that there was no evidence for heterogeneity within the western Pacific subpopulation based on samples from Japan, northern Mariana Islands, Ryukyu Islands, and Palau Islands, and further that the relatively low numbers of skipjack tuna larvae found in the area between long. 170°E and the international dateline in the Northern Hemisphere was supportive of the two subpopulation hypothesis. On the basis of new samples from schools in the western Pacific, which were assigned to either the eastern-central or western subpopulation based on rejection limits for Est 2, Fujino (1972) adjusted the boundary, indicating that the range of the western subpopulation extends out to long. 165°E (between the eastern Caroline Islands and the Marshall Islands/Gilbert Islands) without marked seasonal variation and hypothesized that the Izu-Bonin-northern Mariana Islands complex acts as a barrier to the eastern-central subpopulation. Using the estimated growth rate of skipjack tuna (based on Rothschild 1967), Fujino was able to separate the western subpopulation into A and B components associated with an apparent hatching time in the Northern Hemisphere summer and winter, respectively. Figure 5 depicts the hypothesized range of the western subpopulation, the overlap of northern summer and winter spawning areas, and the migration routes of the A and B units. Subsequently, Fujino (1976) reported some additional results from material collected from the southwestern Pacific. He classified all four schools sampled in New Zealand and one from Tasmania as belonging to the eastern-central subpopulation. From Australia, two schools were classified as belonging to the western subpopulation and one to the eastern-central. Likewise for the New Hebrides (7 schools) and southern Solomons (12 schools), both subpopulations were represented. All schools from New Caledonia (2) and Papua New Guinea (13) were classified as being western subpopulation. Finally, Fujino (1980) presented nonoverlapping Est 2 frequency ranges, namely 0.394-0.570 for the eastern-central and 0.578-0.758 for the western subpopulation. Using these values to classify schools, Fujino found that 40-50% of the schools off eastern Japan in May-June belonged to the western subpopulation and averaged 65% for the entire year. Fujino also indicated that he could subdivide the western subpopulation using a new esterase gene system (EstR) from red blood cells. Taking samples classified as western subpopulation and testing for this new esterase, Fujino found that the Satsunan-Tosa-Kishu group had an average EstR 1 gene frequency of 0.754 and the Bonin-Izu group had an average gene frequency of 0.083. The relationship of these new genetic subpopulations to the previously described A and B units was not stated. Three schools assigned to the eastern-central subpopulation had an average EstR 1 value of about 0.38, thus falling between the two hypothesized western subpopulations.

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[3] Sharp, G. D., and W. P. Kane. Biochemical genetic comparison and differentiation among some eastern Atlantic and Pacific Ocean tropical tunas. Manuscr in prep. U.N., FAO, Fish. Dep., Via delle Terme di Caracalla, 00100 Rome, Italy.

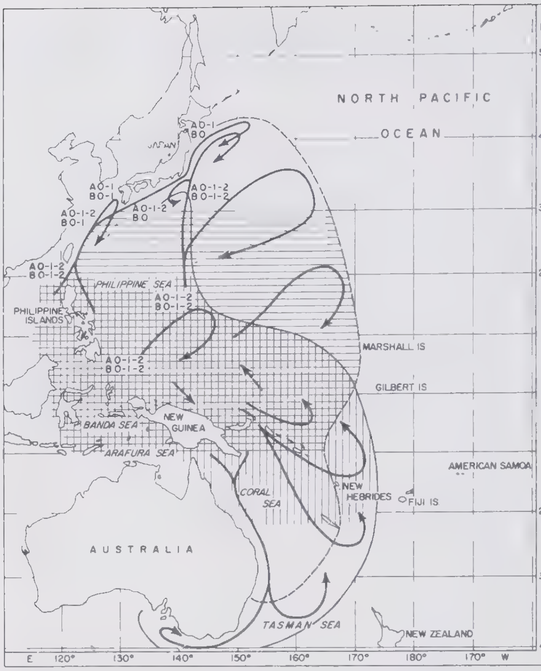

Figure 5.—Distribution and migration routes of the western Pacific skipjack tuna subpopulation proposed by Fujino (1972). Eastern limits of distribution during northern winter and summer are indicated by a solid line and a broken line, respectively. Intensive spawning grounds are shown by horizontal and vertical hatching and migration routes are indicated by curved lines with arrows.

The second approach of determining subpopulations was advanced by Gary D. Sharp who was associated with the Inter-American Tropical Tuna Commission (IATTC) and is now with FAO. Sharp (1978) pointed out that if replicate samples were collected from homogeneous units, one should expect a normal distribution of estimates about whatever parameter was being estimated. He stated, however, that this has not resulted for gene frequencies in the extensive, large-sized samples of both skipjack tuna and yellowfin tuna, *Thunnus albacares*, and argued that this was due to the genetic nonhomogeneity of the schools. As evidence that schools are genetic composites, he referred to his studies on shifts in gene frequency and the clumping of rare alleles in individual schools (Sharp[4]; Sharp and Kane footnote 3). While Sharp (footnote 4) was able to show significant differences between schools based on morphometric discriminant analysis, these differences seemed unrelated to genetic differences. Based on these considerations, Sharp recommended that sample sizes should be on the order of 200 individuals per school. In his study of subpopulations, Sharp placed greater emphasis on the lack of homogeneity of individual schools, compared the distribution of gene frequency estimates among geographical areas, and employed the usual statistical tests for both intra- and inter-area homogeneity.

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[4] Sharp, G. D. Studies of Pacific Ocean skipjack tuna (*Katsuwonus pelamis*) genetics through 1978. Manuscr. in prep. U.N., FAO, Fish. Dep., Via della Terme di Caracalla, 00100 Rome, Italy.

While he indicated that his large-sample data from the eastern tropical Pacific, Papua New Guinea, and New Zealand fit Hardy-Weinberg expectations in all but two cases (in the former site), Sharp (footnote 4) and Sharp and Kane (footnote 3) showed that nearly all sampled schools exhibited statistically improbable clumping of rare alleles or a shift in the estimated gene frequency midway in the length range of the samples, or both. These results indicate not only that the Hardy-Weinberg test is not sensitive to mixtures but that schools tend to be both mixtures of siblings as well as groups with differing gene frequencies. These results cast doubt on the utility of computing average gene frequencies for use in classifying schools to hypothesized subpopulations. Also in testing for homogeneity within geographical areas (eastern tropical Pacific, New Zealand, Papua New Guinea, Hawaii) using his own large samples and the larger sized samples of Fujino's, Sharp (1978, footnote 4) found significant heterogeneity in the esterase system (and in transferrin also, but to a lesser extent). Since tests among areas also show significant heterogeneity, Sharp's results are generally supportive of Fujino's results in that there is evidence for subpopulation differentiation between the eastern-central and western Pacific and within the western Pacific; however, they also indicate that subpopulation differentiation within the eastern-central subpopulation is likely. Sharp's approach then deviates from Fujino's by comparing the similarities of gene-frequency distributions among the various sample sites rather than assigning schools to hypothesized subpopulations based on rejection limits. Thus, Sharp (footnote 4) observed (Fig. 6) that the esterase gene-frequency distribution for Hawaiian samples seems to have components similar to those found in samples off eastern Japan, and other components similar to those in the northern areas of the eastern tropical Pacific and off Ecuador. Also, the typical gene frequency in the eastern tropical Pacific corresponds to the most common gene frequency in Hawaii. For both Palau and Papua New Guinea, there seem to be three groups showing much overlap between the areas. For New Zealand, Sharp says there is one group similar to the eastern Pacific and one unique group, but all of these distributions fall into the upper end of the Hawaiian distribution. The distribution for the northern area of the eastern tropical Pacific is similar to that for Hawaii and contains some components similar to those from Ecuador. The latter was said to have a unique component (with low gene frequency), but this again falls within the range of the Hawaiian samples. Based on all of these findings, Sharp (footnote 4) hypothesized the existence of six subpopulations in the Pacific (Fig. 7). Considerable overlapping of the subpopulation ranges occurs in the central and western equatorial areas.

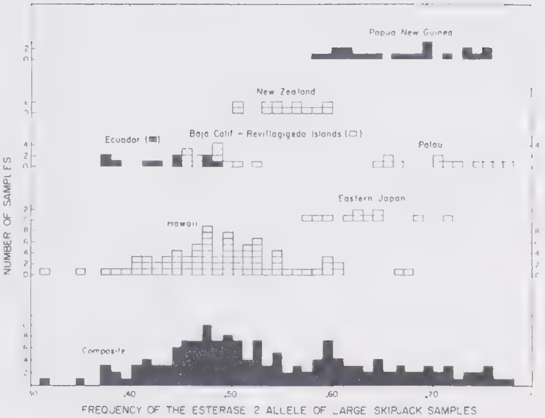

Figure 6.—Frequency distribution of Est 2 skipjack tuna allele for large samples from various sources (from Sharp text footnote 4).

The third approach was used by the SPC in association with their Skipjack Survey and Assessment Programme. Blood samples and various biological information have been collected fairly uniformly across the South Pacific and into the Northern Hemisphere in the western Pacific. With their

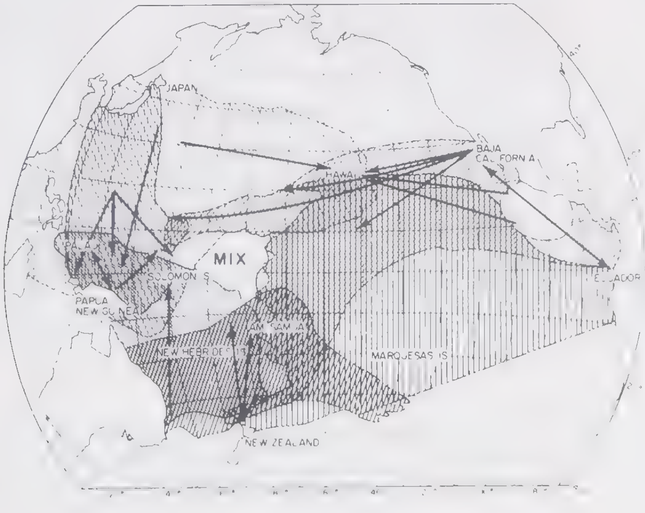

Figure 7.—Ranges of six skipjack tuna subpopulations (from Sharp text footnote 4), with examples of the movement of tagged fish.

interest in determining what effect, if any, population structuring would have on yield and fishery management in the SPC area, they have emphasized the analysis of longitudinal gene-frequency variations and of differences among western, central, and eastern segments (areas A, B, and C) of the SPC.

Having the benefit of much of the research described above, the SPC collected relatively large samples (100 individuals/school), integrated their genetic research with tagging and sampling for size composition, and examined the quantitative aspects of the population genetic methods employed. Thus, they performed certain basic statistical tests of their data before analyzing for subpopulations (South Pacific Commission 1980, 1981), which provided them with the following results. With a sample size of 100, gene frequency of the samples was estimated with a precision of 0.07 at the 95% confidence level. If two genetic populations differ in their gene frequencies by 0.1, they could be statistically separated with a sample size of 25 at a power of 90% (this seems in direct conflict with the results in Fujino 1971). And if over six sample lots (600 individuals) were combined within an arbitrary area, significant heterogeneity was usually found.

Regarding population genetic results, they found that samples from areas A (west of long. 170°E) and B (between long. 170° and 165°E) showed a higher degree of heterogeneity than area C (east of long. 165°E); however, this was based on 76, 32, and 11 sample lots, respectively. Most interestingly, they found a longitudinal cline of Est 2 (Fig. 8) from about long. 140°E (gene frequency of 0.71) to 130°W (gene frequency of 0.37). As would be expected from the results of the tests for heterogeneity for areas A, B, and C, the variance about the cline (regression line) decreased from west to east. To the east of long. 130°W, the cline appeared to cease or to level off. To the west, Lewis[5] felt that the cline continued into the Pacific and Indian Ocean waters of Indonesia, whereas the South Pacific Commission (1981) suggested that the cline may level off. More samples will be needed from the Indian Ocean to resolve this issue.

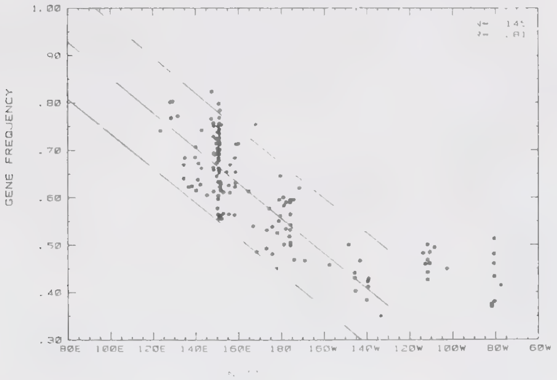

Figure 8.—Relation of esterase gene frequency and longitude. Regression line and 95% prediction limits indicated. Regression excludes samples from east of the SPC area (east of dotted line). N is number of samples; R is correlation coefficient (from South Pacific Commission 1981).

While tagged fish were continuing to be recaptured (and indeed long-term recaptures of many fish tagged in French Polynesia were just being reported), the South Pacific Commission (1980, 1981) attempted to integrate the tagging and genetic experiments. On the basis of the calculated gene frequency of the tagged school, the expected longitudinal range of recapture was estimated from the regression line of gene frequency on longitude. Of the 106 tag recoveries at large for at least 90 d, only 1, released in Kiribati, was recovered in an unexpected area (South Pacific Commission 1980). Then, regressing the net west-east movement of all tagged fish from each school for which gene frequency was estimated (29 schools) against the difference between calculated gene frequency of the school and the gene frequency estimated from the cline, they failed to find a significant relationship (South Pacific Commission 1981). A positive relationship would have indicated that fish tended to migrate to areas having schools with average gene frequencies more similar to that of schools in which they were at the time of tagging. While this second test may seem to be more critical, it may be biased because it includes short-term recaptures which tend to disperse very little and because fish tagged in the western perimeter of the Pacific basin may be restricted in their migration to the west.

Returning to serum transferrin, Fujino and Kang (1968b) stated that the system was independent of sex and, later, of the blood groups C, B, and Y (Fujino 1970a). They found no evidence for heterogeneity either within or among the central-eastern Pacific, Atlantic (also shown by Fujino 1969), and western Pacific areas. However, when they grouped the data by areas, the pooled data showed an excess of heterozygotes compared with Hardy-Weinberg expectations. They presented data purportedly showing that the frequency of certain alleles varied with size and hypothesized that differential mortality with size could maintain the balanced polymorphism. Subsequently, however, Sharp and Kane (footnote 3), using larger sample-size lots collected in the eastern tropical Pacific and off New Zealand, found that most samples fitted Hardy-Weinberg proportions. Reexamining Fujino's data, they showed that only one size group out of five deviated from Hardy-Weinberg proportions. Lewis (footnote 5) reported that samples collected from Pacific and Indian Ocean waters of Indonesia had transferrin frequencies falling within the normal range seen in all other historical samples. Presenting results from samples collected all across the South Pacific, as well as from certain sites in the western North Pacific, the South Pacific Commission (1980) found no variation of transferrin gene frequency with longitude. By plotting the variation of the frequency of the major transferrin allele against those for the major esterase allele, the variations were shown to be independent and the variation for transferrin was the smaller of the two by far. The gist of all of these studies is that transferrin has not proven useful in differentiating subpopulations of skipjack tuna.

(4) Tissue isoenzymes

Sprague (1970) found as many as 12 esterase activity bands in samples of dark and light skeletal muscle, heart muscle, kidney, liver, spleen, gonad, brain, and whole blood collected from skipjack tuna in Hawaiian waters. These 12 bands appear to be arranged in 6 regions, but only 2 of the regions were hypothesized to compose a genetic system. The fourth region contained serum esterases as described in the previous section. Sprague contended that the esterases in region 5 were also usable for subpopulation studies, but insufficient data were available at the time to do so. He hypothesized that the three observed phenotypes in this region are coded by two alleles. McCabe and Dean (1970) also found innumerable bands of esterase activity in samples of liver and skeletal muscle taken from skipjack tuna in the Atlantic Ocean. They indicated that the esterases in only two activity regions, Est Ib and Est III, were stable and, therefore, usable for subpopulation studies carried out in the field. Region Est III seemed to be a dimer system made up of four phenotypes coded by four alleles. Since one of the alleles had a frequency of 0.964, this esterase system is, for practical purposes, monomorphic and not likely of much use in studying subpopulations in the Atlantic Ocean; however, the situation in the Indian and Pacific Oceans could prove to be different. In region Est Ib, they observed 15 phenotypes in 300 samples and hypothesized that the phenotypes were coded by 7 alleles. No specific data were given, nor was it shown that the system was amenable to Hardy-Weinberg analysis. Nonetheless, Est Ib may have potential for use in determining subspecific differentiation, since no single allele had a frequency > 0.4. Unfortunately, the phenotypes must be determined by a two-stage electrophoresis process, making the process more complicated and expensive than is the case with serum esterases.

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[5] Lewis, A. D. Undated. Report, Collection of biological material from skipjack (*Katsuwonus pelamis*) and other scombrids for genetic analysis. Indonesia, 9-23 December, 1979. Typescript, no pag. Australian National University, Department of Population Biology. Ministry of Agriculture, Forests, and Fisheries, Fisheries Division, Suva, Fiji.

McCabe et al. (1970) tested for dehydrogenase, acid phosphatase, and alkaline phosphatase activity in skeletal muscle sampled from skipjack tuna and reported finding polymorphisms of 6-phosphogluconate dehydrogenase (6-PGD) and alpha-glycerophosphate dehydrogenase (α-GPD) polymorphism in liver samples. The 6-PGD system was found to be a dimer with four phenotypes coded by four alleles, and the α-GPD system was found to consist of three phenotypes coded by three alleles. Since the frequency of PGD and α-GPD were both over 0.9, both systems are essentially monomorphic in the Atlantic and would probably not be useful for studying population differentiation in that ocean; however, the systems could prove to be useful in the Pacific and Indian Oceans.

Lewis (footnote 5) reported preliminary results from his investigation of 21 enzymes, encoded by 25 presumed gene loci, in liver tissues collected from skipjack tuna in north Queensland, Australia, and Padang, Indonesia. Only the adenosine deaminases ADA1 and ADA2 and guanine deaminase (GDA) were found to be sufficiently polymorphic (five, four, and three alleles, respectively) to encourage further research, whereas glucose phosphate isomerase (GPI), mannose phosphate isomerase (MPI), 6-PGD, isocitrate dehydrogenase (ICD), α-GPD, sorbitol dehydrogenase (SORD), glutamate oxaloacetate transaminase (GOT1 and GOT2), phosphoglucomutase (PGM1 and PGM2), peptidase 1 and 2, malic enzyme (ME1 and ME2), fumarate hydratase (FH), malic dehydrogenase (MDH), lactic dehydrogenase (LDH), pyruvate kinase (PK), glutamate pyruvate transaminase (GPT), 6-phosphofructokinase (PFK), phosphoglycerate kinase (PGK), and superoxide dismutase (SOD) were found to be absolutely or essentially monomorphic. No large differences were evident between the Australian and Indonesian material for ADA or GDA, but the samples from Indonesia seemed to be homogeneous and had a lower gene frequency than the samples to the east. The South Pacific Commission (1981) found a decreasing cline in gene frequency for the GDA$_1$ allele from west to east (Fig. 9).

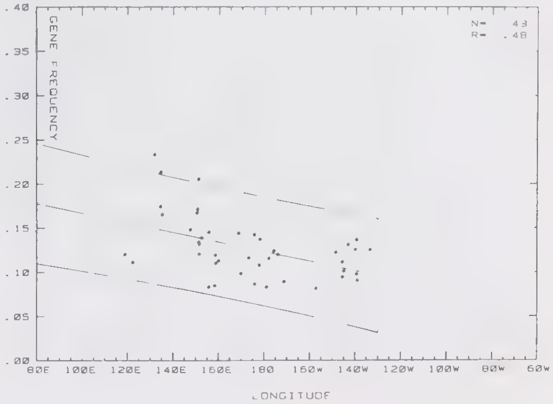


Figure 9.—Relation of guanine deaminase gene frequency and longitude. Regression line and 95% prediction limits indicated. Regression excludes samples from east of the SPC area (east of dotted line). N is number of samples; R is correlation coefficient (from South Pacific Commission 1981).

2 DISTRIBUTION

2.1 Total area

Prior to 1959, the occurrence and distribution of the skipjack tuna had been determined essentially from records of captures in coastal waters and in those offshore areas subjected to commercial pole-and-line and purse seine fishing. Because pole-and-line fisheries were constrained by distance to areas within easy access of bait supplies and purse seine fisheries were confined to those areas with a relatively shallow mixed layer, a characteristic of the purse seine fishery in the eastern sides of both the Atlantic and Pacific Oceans (Brock 1959), there were large gaps in our knowledge about the distribution of skipjack tuna in midoceanic areas of the Pacific Ocean. Even less was known about the occurrence and distribution of skipjack tuna in the Indian and Atlantic Oceans, where fishing for this species on a commercial scale had not developed as in the Pacific Ocean.

Since 1959 various authors (Brock 1959; Kasahara 1968; Miyake 1968; Marcille and Suzuki 1974; Matsumoto 1974, 1975) have utilized the Japanese tuna longline data to determine the distribution of skipjack tuna in midoceanic areas. Although the catches made by the longline gear were small, they constituted proof of the presence of skipjack tuna and the information thus obtained has expanded our knowledge about the distribution of the species.

The distribution of skipjack tuna (Fig. 10) was derived from atlases of the Japanese tuna longline catch data for various years from 1964 to 1979 ([Japan.] Fisheries Agency 1967a, b, 1968, 1969, 1971, 1972, 1973, 1979a, 1980a, 1981), the Japanese southern water fishery for various years from

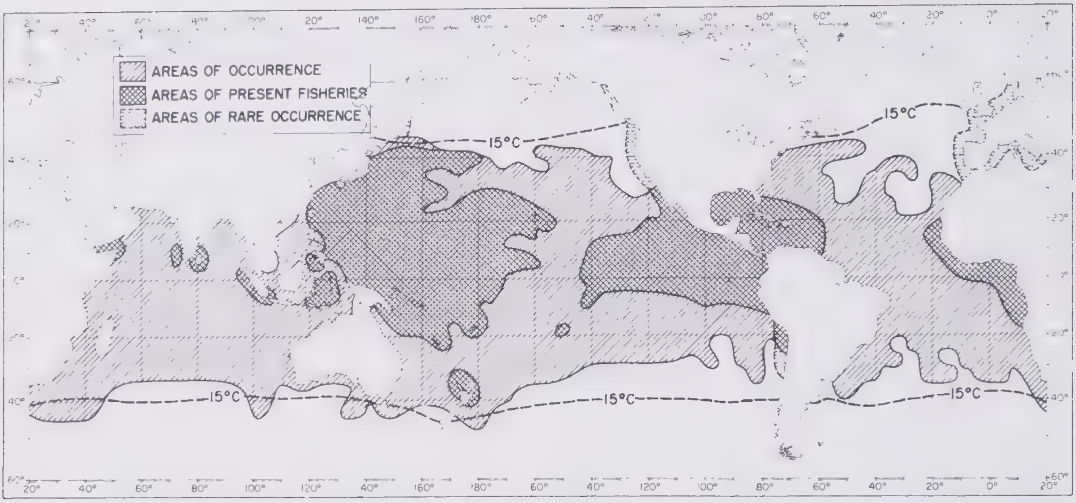


Figure 10.—Skipjack tuna distribution and fisheries in the major oceans. The mean 15 °C isotherms represent maximum late summer poleward displacement (data from various sources).

1964 to 1979 (Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory (Tohoku RFRL) undated a, b, c, d) the Japanese skipjack tuna bait boat fishery catch data for 1977 and 1978 ([Japan.] Fisheries Agency 1979b, 1980b), and other sources (Wade 1950; Robins 1952; Brock 1959; Roux 1961; Jones and Silas 1963; Postel 1963; Sakagawa 1974; Calkins 1975; Sakagawa and Murphy 1976; Santos 1978; Kikawa and Higashi 1979; Habib et al. 1980a, b, c; Blackburn and Serventy 1981). The species occurs continuously from east to west across all oceans, and over a wide latitudinal range from about lat. 45 °N to south of 45 °S in the western Pacific and from about lat. 30 °N to 30 °S in the eastern Pacific. In the Atlantic Ocean, skipjack tuna have been caught from about lat. 45 °N to 40 °S in the western side and from lat. 35 °N to south of 40 °S in the eastern side. Rare captures off Vancouver Island (Clemens and Wilby 1946) in the Pacific Ocean and off the British Isles, Scandinavia, and Denmark (Postel 1963) in the Atlantic Ocean extend the limits of occurrence northward to lat. 49 °N in the eastern Pacific and beyond lat. 55 °N in the eastern Atlantic. Skipjack tuna have been taken as far south as lat. 40° to 45 °S in the western Indian Ocean and south of Australia, and, although not indicated in Figure 10, in the eastern part of the Persian Gulf on rare occasions. The species occurs also in the Mediterranean Sea, from Gibraltar to Italy, but not in large concentrations as in the Atlantic Ocean (Belloc 1955).

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Larvae of skipjack tuna have been found over a wide area in all the major oceans, including the Gulf of Mexico and throughout the Indo-Pacific Archipelago (Fig. 11). The known distribution of skipjack tuna larvae in the western and cen-

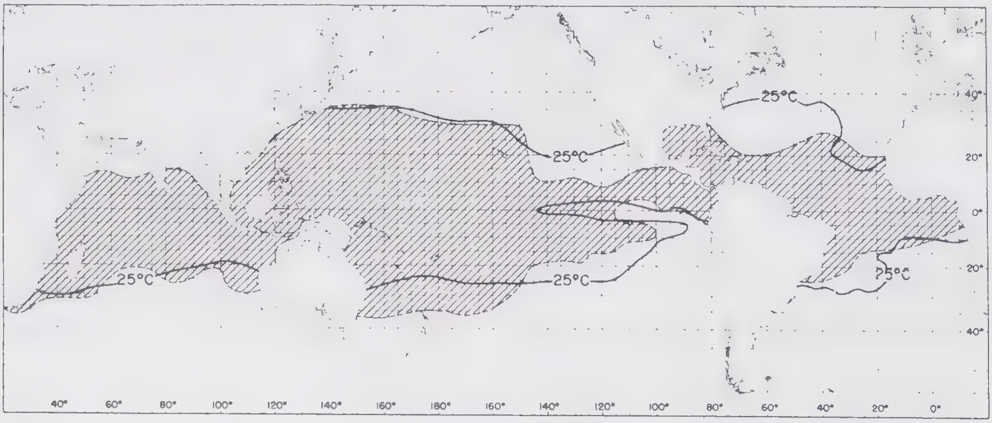


Figure 11.—Distribution of skipjack tuna larvae, 1952-75 (data from various sources).

tral Pacific extends from near lat. 35°N off Japan to as far south as lat. 37°S, off the southeastern part of Australia (Matsumoto 1958; Nakamura and Matsumoto 1967; Ueyanagi 1969, 1970; Mori 1970; Seckel 1972; Chen and Tan 1973; Nishikawa et al. 1978), and in the eastern Pacific from lat. 15°N to 5°S (Klawe 1963; Love 1970, 1971, 1972, 1974). The distribution in the Pacific is broad latitudinally in the west but narrow in the east due to the constriction of warm water favorable for spawning by cold currents flowing toward the Equator in both hemispheres. Both northern and southern boundaries shown may well represent the limits of distribution of skipjack tuna larvae in that ocean.

In the Indian Ocean, the distribution of larvae extends southward to the southern tip of Africa, to about lat. 36°S, and unlike that in the Pacific Ocean, larvae have been taken in the eastern part of the ocean from as far south as lat. 30°S (Ueyanagi 1969). The northern boundary is limited to lat. 11° to 15°N by the Asian Continent (Jones 1959; Gorbunova 1963, 1965a; Jones and Kumaran 1963; Ueyanagi 1969).

The distribution in the Atlantic Ocean differs somewhat from that in the Pacific Ocean. Although the distribution is wider in the western side, the southern boundary does not reach much beyond lat. 25°S and the northern boundary does not extend beyond lat. 30°N (Klawe 1960; Suarez Caabro and Duarte-Bello 1961; Gorbunova and Salabarría 1967; Richards 1969; Zhudova 1969; Richards and Simmons 1971; Ueyanagi 1971; Juarez 1974; Nishikawa et al. 1978). The large dip in the northern boundary in the region of the Sargasso Sea may be due to infrequent sampling. The distribution of larvae in the eastern sector of the ocean differs from that in the Pacific Ocean. Whereas the distribution narrows and the concentration of larvae diminishes greatly in the eastern Pacific (Klawe 1963), the distribution is broader and the abundance of larvae is much greater (Richards and Simmons 1971) in the eastern Atlantic Ocean.

Within the vast range over which the larvae are distributed, certain areas of high abundance can be recognized. Kawasaki (1965a) suggested that the center of abundance of skipjack tuna larvae in the Pacific Ocean was in the area bounded by lat. 5°N and 4°S and long. 160°E and 140°W. He later (1972) revised his western boundary to long. 120°E, on the basis of Ueyanagi's (1969) data, which showed a peak in larval abundance at long. 120°-150°E along a band of water from lat. 10°N to the Equator. Matsumoto (1975), after adjusting the catches of larvae made with different sized nets and different towing methods in a band of water from lat. 10°S to 20°N (Table 3; Fig. 12), reported that the center of larval skipjack tuna abundance was between long. 160°E and 140°W (similar to Kawasaki's first estimate), that the abundance was moderate between long. 100° and 140°W and between long. 120° and 160°E, and low in the eastern Pacific east of long. 100°W.

Other areas north of lat. 20°N with relatively high larval abundance include the waters around the Hawaiian Islands, where the catches in night surface tows with a 1 m net during the spawning season averaged 4.1 larvae/tow (data from Seckel 1972) and waters to the south of Japan between lat. 25° and 30°N, where the catches in subsurface tows (20-30 m) with a 2 m net averaged nearly 4.0 larvae/tow (Ueyanagi 1969, fig. 22, Area A).

In the Atlantic Ocean, larvae are apparently more abundant in the eastern half of the ocean between lat. 10°N and

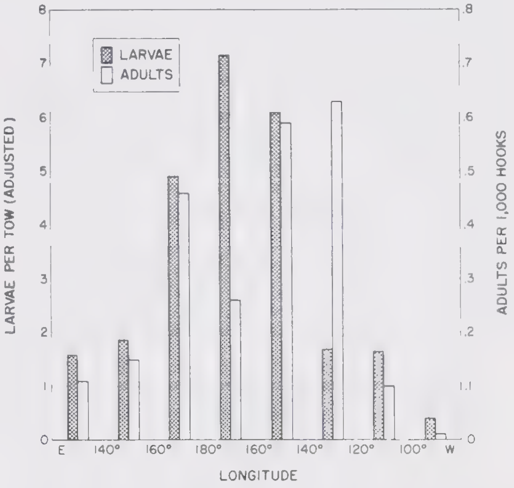


Figure 12.—Catch rates of skipjack tuna larvae and adults by longitude in the Pacific Ocean between lat. 10°S and 20°N (from Matsumoto 1975).

Table 3.—Catch rates of larval skipjack tuna in night surface tows from the Pacific Ocean (from Matsumoto 1975).

Longitude	Latitude	Quarter sampled	Net diameter (m)	Duration of tow (min)	Number of tows	Total larvae (no.)	Conversion factor[1]	Adjusted catch	Adjusted larvae per tow
80°-100°W	4°-15°N	I, II	1	30	33	7	[2]1.836	12.85	0.39
100°-120°W	10°-15°N	II	1	30	10	11	[2]1.836	20.20	1.63
100°-120°W	0°-7°S	I	1	30	12	19	[3]0.827	15.71	
120°-140°W	10°S-10°N	I, IV	1	30	21	42	[3]0.827	34.73	1.65
140°-160°W	10°S-20°N	I, III	1	30	32	239	[3]0.827	195.18	6.10
160°W-180°	10°S-20°N	I, II, III	1	30	45	389	[3]0.827	321.70	7.15
160°E-180°	10°S-20°N	I, III	1	30	6	45	[3]0.827	37.22	4.94
160°E-180°	10°S-20°N	II, IV	2	20	44	560	[4]0.375	210.00	
140°-160°E	10°S-20°N	II, III, IV	2	20	112	562	[4]0.375	210.75	1.88
120°-140°E	0°-20°N	II, IV	2	20	141	581	[4]0.375	217.88	1.54

[1] Conversion factor is the ratio of standard to average volume of water strained. Standard volume used was 1,454 m^3, the volume strained by a 1 m net towed at 2.0 kn for 30 min.

[2] Computed from average volume of 79 m^3 from 62 tows. Data from Klawe (1963)

[3] Computed from average volume of 1,759 m^3 from 289 tows. Data from NMFS Honolulu Laboratory files and Strasburg (1960)

[4] Computed from estimated volume of 3,878 m^3 at constant towing speeds of 2 kn. Catch data from Ueyanagi (1969)

10°S (Richards 1969). There are no other reports from the Atlantic or the Indian Oceans providing measures of abundance.

Juvenile skipjack tuna are rarely seen at sea and are extremely difficult to capture. They have been collected in various types of trawl and plankton nets, by dip netting at night under light, and from stomach contents regurgitated by seabirds, but the greatest number have come from stomachs of tunas and billfishes.

The relatively small number of recorded captures attest to the difficulty in capturing the juveniles. Higgins (1967) compiled all records of 512 juveniles, 1.2 to 30 cm in length, taken from the Pacific for the period 1916-66. Yoshida (1971) obtained 1,742 juveniles, 1.6 to 40 cm in length, from the stomachs of billfishes from Hawaiian and central South Pacific waters in the period 1962-66. Higgins (1970) examined 578 "juveniles," 7 mm to 4.7 cm in length, taken in midwater trawls in Hawaiian waters. Roughly 40% of the latter catch consisted of skipjack tuna larvae < 1.2 cm in length. Simmons (1969) compiled records of 163 juveniles, 13 to 15 cm in length, taken by various methods, including samples from stomach contents regurgitated by seabirds, from the Atlantic Ocean. Mori (1972) examined 5,851 juveniles and young, 3 to 35 cm in length including some adults to 70 cm, from stomachs of tunas and billfishes taken from the Pacific, Indian, and Atlantic Oceans during the period 1949-69. Of this number, 4,104 were juveniles < 35 cm in length: 3,778 from the Pacific Ocean, 202 from the Indian Ocean, and 124 from the Atlantic Ocean. Thus, the total juvenile skipjack tuna collected from 1916 through 1969 is < 7,000, of which roughly 300 were from the Atlantic Ocean, 200 from the Indian Ocean, and the remainder from the Pacific Ocean. Despite the small numbers of juveniles collected from the Indian and Atlantic Oceans, the dispersion of the capture sites presents a fair coverage of the two oceans.

The above data show that juvenile skipjack tuna are widely distributed in the tropical and subtropical waters of all oceans (Fig. 13). In the Indian Ocean the distribution extends from lat. 15°N to 35°S. In the Pacific Ocean the distribution extends generally from lat. 35°N to 35°S in the west and narrows to lat. 10°N and 5°S in the east. In the Atlantic Ocean the distribution extends from lat. 40°N in the west to lat. 30°S in the east. In all oceans the pattern of distribution resembles that of the larvae. From information acquired recently about the extremely rapid growth of skipjack tuna and other tunas reared from artificially fertilized eggs through the juvenile stages (Harada et al. 1971; Mori et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973; Ueyanagi et al. 1973), it would be expected that juveniles of skipjack tuna occur in all localities where larvae have been found.

In certain localities, i.e., North and South Atlantic, central Indian, and northwest and southeast Pacific, the distribution of juveniles is shown to extend beyond the range indicated for the larvae. This could be due to juveniles leaving the immediate spawning area as they grew larger and became more mobile. Mori (1972) suggested that this could occur when the juveniles attain the length of 30 cm.

2.22 Adults

Excluding those areas from which only rare captures have been reported, the distribution of skipjack tuna shown in Figure 10 (medium shaded areas) shows the maximum northward and southward limits. Both boundaries vary seasonally and annually as the skipjack tuna respond to seasonal changes in the environment. The boundaries generally shift poleward in the summer and fall as seasonal warming of the water occurs in higher latitudes and recede toward the Equator in winter and spring as the water cools. However, the northern and southern boundaries do not appear to shift in unison with each other and the north-south shifting of the boundaries does not occur simultaneously across the ocean, due to the varying effects of warm and cold currents in different parts of the oceans.

Matsumoto (1975) has shown that in the Pacific Ocean the northern boundary moves poleward in the third and fourth quarters and recedes toward the Equator in the first and second quarters (Fig. 14). The shift occurs at about the same time in both the western and eastern halves of the ocean. In

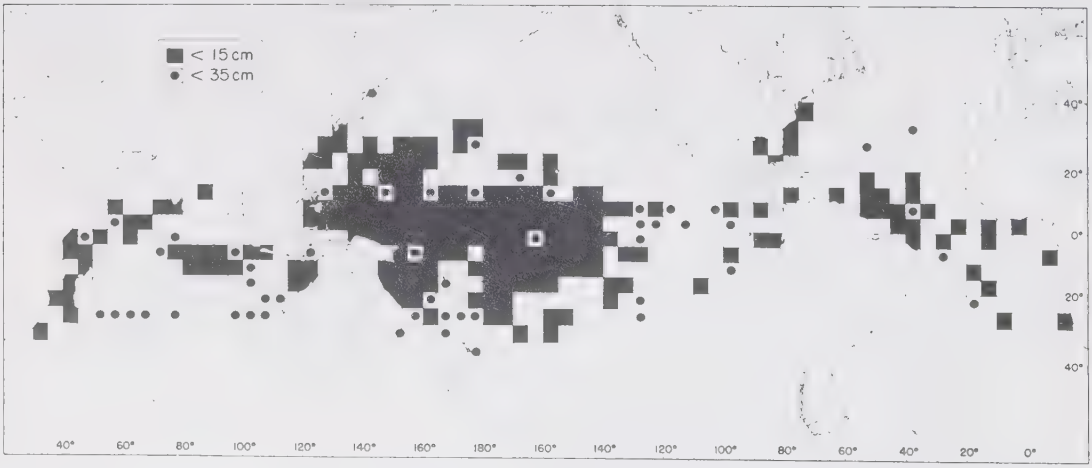
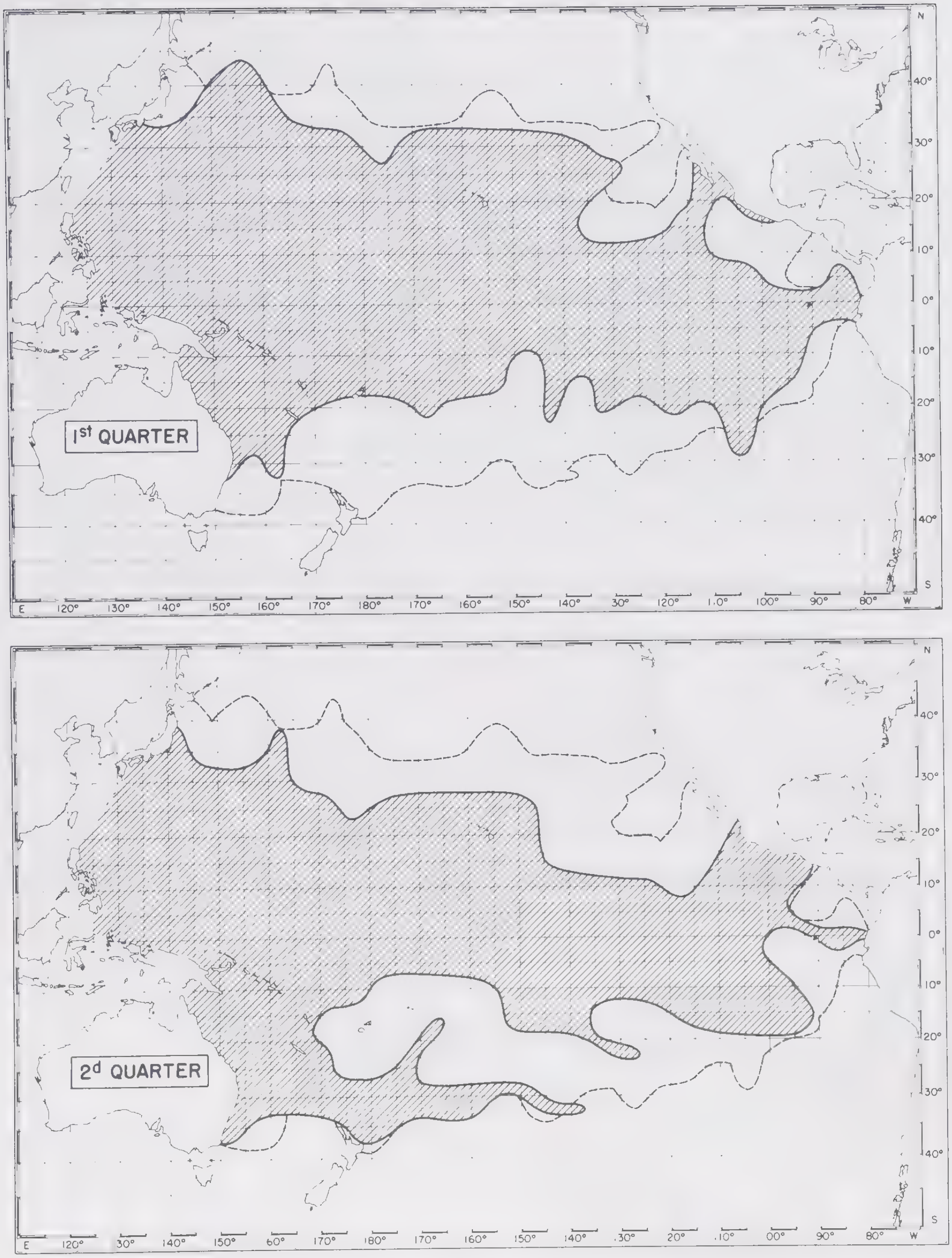


Figure 13.—Locations of known captures of juvenile skipjack tuna in the major oceans from 1916 through 1969 (data from various sources).


1st QUARTER
2d QUARTER
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170°
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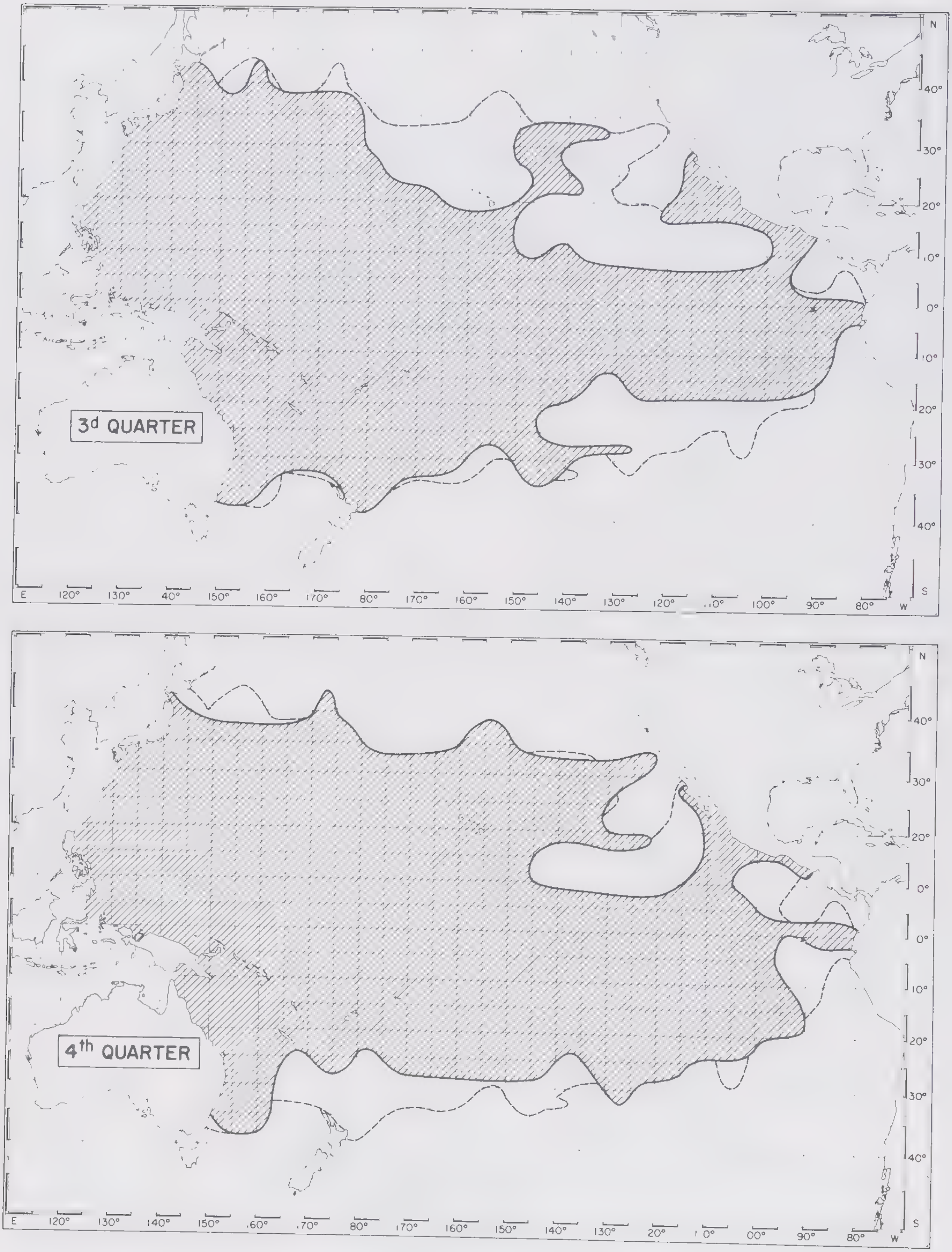
140°
130°
120°
110°
100°
90°
80°
W

Figure 14.—Outlines of the northern and southern boundaries of skipjack tuna caught in the Japanese tuna longline fishery, 1964-67, by yearly quarters (shaded area). The broken lines denote the maximum range for all four quarters (from Matsumoto 1975).


3d QUARTER
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W

Figure 14.—*Continued.*

the Southern Hemisphere, however, the western half of the boundary moves poleward in the second and third quarters and toward the Equator in the fourth and first quarters, whereas in the eastern half, the shifting of the boundary occurs about 3 mo later. Although similar studies have not been made in other oceans, we believe that the boundaries of skipjack tuna distribution in those oceans also undergo similar changes.

Within this wide distributional range, adult skipjack tuna occur in varying densities in different parts of the oceans, with areas of moderate to high densities quite often being defined by the existence of a fishery (darkly shaded areas, Fig. 10). In the Indian Ocean, skipjack tuna fisheries occur in the Gulf of Aden and the vicinity of Laccadive Islands, Maldive Islands, and Sri Lanka, and sporadically along the coastlines of countries bordering the ocean from Australia across the Indian subcontinent to South Africa. In the western Pacific Ocean skipjack tuna fisheries occur in the vicinity of Japan, Ryukyu Islands, Taiwan, Philippines, Bonin Islands, Mariana Islands, Caroline Islands, Palau Islands, Papua New Guinea, Solomon Islands, New Caledonia, Australia, and New Zealand. In the north along lat. 40° to 45°N, the fishery extends eastward to long. 176°W. In the Equatorial Countercurrent and North Equatorial Current the fishery extends eastward to long. 154°W. In the central Pacific Ocean, fisheries occur around the Hawaiian Islands and French Polynesia. In the eastern Pacific Ocean, fisheries occur off Baja California, the Revillagigedo Islands, Clipperton Island, Central America, Cocos Island, the Galapagos Islands, and northern South America. The fisheries extend westward along the equatorial currents to long. 140°W. In the Atlantic Ocean, fisheries occur in the Gulf of Mexico, the Caribbean Sea, around Cuba, and off Africa between lat. 20°N and 15°S.

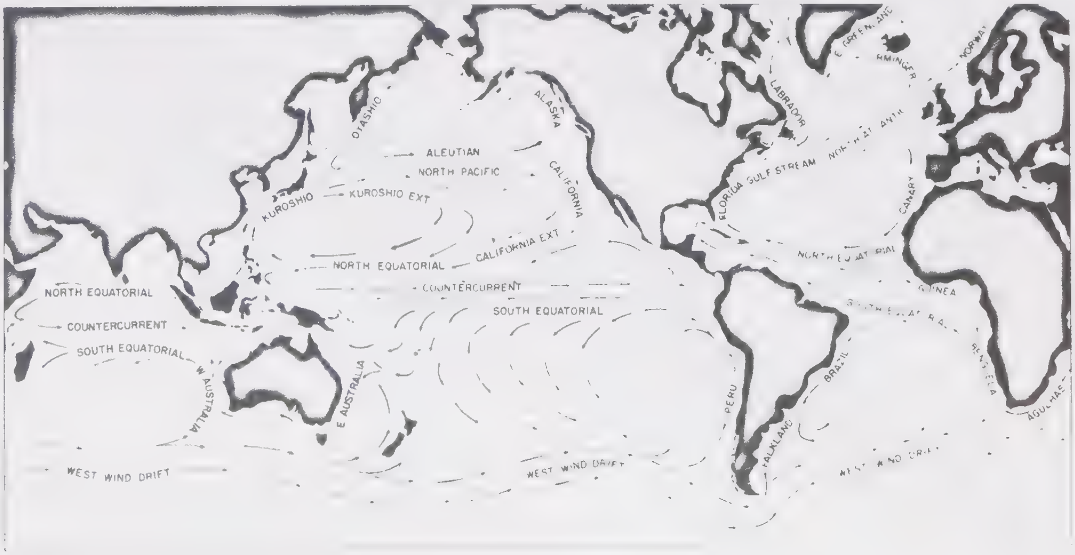
2.3 Determinants of distribution changes

2.31 Larvae and juveniles

Surface currents influence the distribution of skipjack tuna larvae indirectly by modifying the distribution of sea-surface temperatures (Brock 1959; Blackburn 1965). In both the Atlantic and Pacific Oceans the warm North and South Equatorial Currents flow westward and are deflected poleward as they reach the continents. Cold currents at high latitudes flow eastward and are deflected toward the Equator upon reaching the western shores of the continents (Fig. 15). This results in the expansion of the warm water area favorable for spawning in the west and the restriction of similar area in the east, as shown by the 25°C isotherm in Figure 11. A similar situation exists in the Indian Ocean, except that it applies only to the Southern Hemisphere.

Currents can directly influence the distribution of skipjack tuna larvae by transporting the eggs during the incubation period and early growth stages of the larvae. However, such influence is localized and not easily discernible because it is overshadowed by the extensiveness of the spawning area and the length of the spawning season. Even around islands, where the currents are modified to form wakes and eddies (Barkley 1972) in which zooplankton and fish larvae can be entrapped, skipjack tuna larvae were found to be randomly distributed (Nakamura and Matsumoto 1967; Powles 1977).

Skipjack tuna, as well as other tunas, require warm water for spawning and larval survival; consequently, the limits of larval distribution are governed largely by water temperature. The range of distribution can be described roughly by the location of the mean 25°C surface isotherm (Fig. 11). Others (Ueyanagi 1969; Mori 1972) have used the 24°C isotherm to describe the distributional range. This does not imply that


OYASHIO
ALASKA
ALEUTIAN
NORTH PACIFIC
CALIFORNIA
KUROSHIO
KUROSHIO EXT
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SOUTH EQUATORIAL
NORTH EQUATORIAL
COUNTERCURRENT
SOUTH EQUATORIAL
W AUSTRALIA
E AUSTRALIA
WEST WIND DRIFT
WEST WIND DRIFT
E GREENLAND
IRMINGER
NORWAY
LABRADOR
FLORIDA
GULF STREAM
NORTH ATLANTIC
CANARY
NORTH EQUATORIAL
GUINEA
SOUTH EQUATORIAL
BENGUELA
AGULHAS
BRAZIL
PERU
FALKLAND
WEST WIND DRIFT

Figure 15.—Ocean current systems (from Brock 1959).

skipjack tuna larvae are not found in water temperatures below 25° or 24°C, for they have been take at surface temperatures as low as 22.1°C (Matsumoto 1974).

Both the optimum and minimum temperatures for skipjack tuna larvae differ by areas (Table 4). In the western Pacific Ocean between lat. 30°N and the Equator, all larvae taken in surface night tows from 10 cruises of the RV *Shoyo Maru* (data from Ueyanagi 1969) were from waters 25° to 29°C. The most productive tows, in occurrence and number of larvae, were made in 28°C water. The lowest and highest temperatures in which skipjack tuna larvae were caught were 23.5° and 30°C, respectively. These larvae were taken in subsurface tows at 20-30 m (not included in table). In the vicinity of the Hawaiian Islands between lat. 10° and 26°N (Table 3), nearly all larvae caught in surface night tows from nine cruises of the RV *Townsend Cromwell* in 1964 and 1965 (unpubl. data, Honolulu Laboratory), were from waters 23°-26°C, and the most productive tows, in occurrence and number of larvae, were in 25° and 24°C water, respectively. The coldest water in which skipjack tuna larvae were caught was 22.1°C. Strasburg (1960), using opening and closing plankton nets towed obliquely at 0-60, 70-130, and 140-200 m in the equatorial central Pacific, reported the capture of a skipjack tuna larva (Fig. 16) in water well below 65°F (18.5°C) and felt that 60°F (15.6°C) was the minimum temperature in which tuna larvae could occur.

Studies of tuna larvae taken in plankton nets by others (Matsumoto 1958; Strasburg 1960; Klawe 1963; Ueyanagi 1969; Richards and Simmons 1971) have shown that skipjack tuna larvae generally are limited to the upper 50 m of water, that they undergo vertical diel migration, and that the vertical migration is most pronounced in the upper 30 m. All of these studies show that surface tows at night caught considerably more larvae than day tows. Although Strasburg's results (Fig. 16) suggest that larvae may be present below the thermocline, Klawe (1963) reported that none were taken below the mixed layer in the eastern Pacific Ocean.

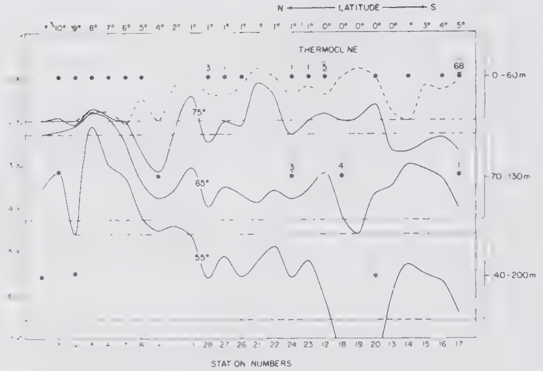

Figure 16.—Isotherm and thermocline depths at closing net plankton stations in the central equatorial Pacific Ocean (lat. 11°N-5°S; long. 140°W), *Hugh M. Smith* cruise 33. Circled numbers denote skipjack tuna larvae, dots represent closing net tows yielding other tuna larvae (modified from Strasburg 1960).

Juvenile skipjack tuna (up to about 47 mm) also are found near the surface. Sampling for juvenile tunas with a small mesh midwater trawl, Higgins (1970) found that shallow tows (maximum depth of 20 m) at night tended to catch the most juveniles and deep tows (100 m) at night, the fewest. Catches during the morning were not significantly different from those at night, but shallow morning tows tended to be less productive than shallow night tows, and deep morning tows tended to be more productive than deep night tows. Daytime catches were about the same in shallow and deep tows. The differences in the catch rates for juvenile skipjack tuna between shallow and deep tows at different times of the day were assumed to be the result of diel vertical migration.

Higgins (1970) found also that juvenile skipjack tuna were significantly larger in deep tows than in shallow tows, and night and morning tows at the deeper depth also tended to catch larger juveniles than day tows. He tentatively concluded that the smaller juveniles live primarily in the upper isothermal layer, whereas the larger juveniles tend to occur in or migrate to deeper water.

2.32 Adults

(1) Surface temperature

The temperature range within which skipjack tuna appear to be restricted has been reported on a world scale by Laevastu and Rosa (1963) as 17° to 28°C and 19° to 23°C for the major fisheries. Specific regions of the world oceans not only show some variations, but extend the range further. Uda

Table 4.—Skipjack tuna larvae taken in surface tows during 10 cruises of the *Shoyo Maru* in the western North Pacific Ocean (Ueyanagi 1969) and in 9 cruises of the *Townsend Cromwell* in the central North Pacific Ocean (unpubl. data, NMFS Honolulu Laboratory).

	Western Pacific (lat. 30°N-0°)				Central Pacific (lat. 10°-26°N)[1]			
Surface temp. (°C)	Number tows	Number larvae	Percent occurrence	Larvae per tow	Number tows	Number larvae	Percent occurrence	Larvae per tow
20	3	0	0	0	1	0	0	0
21	6	0	0	0	1	0	0	0
22	10	0	0	0	14	11	42.8	0.79
23	5	0	0	0	29	88	58.6	3.04
24	15	0	0	0	46	192	56.5	4.17
25	27	15	25.9	0.56	38	157	65.8	4.13
26	66	109	47.0	1.65	31	74	61.3	2.38
27	109	260	46.7	2.38	5	3	20.0	0.60
28	119	611	50.4	5.13	—	—	—	—
29	92	217	31.6	2.36	—	—	—	—
30	6	1	16.6	0.17	—	—	—	—

[1] Includes only tows made during the spawning season, March-September.

(1957) gave the range off Japan as 17.5° to 30°C for all occurrences; Broadhead and Barrett (1964) and Williams (1970) reported a range of 17° to 30°C in the eastern Pacific Ocean; Jones and Silas (1963) reported regular catches of skipjack tuna off southern India from 27° to 30°C water; Robins (1952) reported skipjack tuna taken in temperatures of 14.7° to 20.8°C in Tasmanian waters; and Eggleston and Paul (1978) gave a range of 16° to 22°C off New Zealand. Thus, the overall temperature range of skipjack tuna occurrence could be taken as 14.7° to 30°C. Figure 10 shows that the 15°C isotherm adequately demarks the range of skipjack tuna occurrence. (Note: The 15°C isotherms shown were for the warmest month of the year in both hemispheres and, hence, represent the maximum average poleward displacement.)

As in the distribution of the larvae, temperature plays an important role in the distribution of the adults. Its influence is usually not obvious in the tropics, where the temperature is relatively uniform throughout the year, but is most noticeable at the higher latitudes. This is readily seen in the persistence throughout the year of high catch rate cells of skipjack tuna taken on the tuna longline in the equatorial Pacific, as compared with the latitudinal shifting of such cells near the northern and southern boundaries of distribution in response to seasonal changes in temperature (Matsumoto 1975), and in the marked seasonality seen in the surface fisheries near the northern and southern limits of distribution in the northeastern and southeastern Pacific, Hawaii, northwestern Pacific, Papua New Guinea, and New Zealand (Kawasaki 1965b; Joseph and Calkins 1969; Uchida 1975; Habib 1976, 1978; Forsbergh 1980; Habib et al. 1980a, b, c; Wankowski 1980).

That skipjack tuna seek preferred temperatures is indicated by catch patterns in the various fisheries. These temperatures vary by regions: 20° to 24°C in the northwestern Pacific fishery (Uda 1957), 20° to 30°C in the eastern Pacific fishery (Williams 1970), 28° to 29°C off southern India (Jones and Silas 1963), 16° to 18°C off Tasmania (Robins 1952), and 19° to 21°C off New Zealand (Eggleston and Paul 1978). Sharp (1978) listed the optimum temperature range of commercial activities and schooling behavior of skipjack tuna for five hypothesized subpopulations in the Pacific Ocean as follows: northeastern Pacific, 20°-26°C; southeastern Pacific, 20°-28°C; New Zealand, 17°-23°C; Papua New Guinea-Solomon Islands, 28°-30°C; and northwestern Pacific, 20 -28°C. Others who have investigated the relationship of skipjack tuna and water temperature include Kuroda (1955), Kawasaki (1958, 1965a), Schaefer (1961b), Radovich (1963), Kasahara and Tanaka (1968), Uchida (1970), Seckel (1972), and Yasui and Inoue (1977).

(2) Salinity

According to Blackburn (1965), "Salinity measurements can be important in characterizing and detecting oceanic features with which tuna are associated but salinity *per se* has no known direct effect on tuna distribution." Barkley (1969), however, showed that the habitat of adult skipjack tuna in the Pacific Ocean appears to coincide geographically with areas where a shallow salinity maximum is present seasonally or throughout the year (Fig. 17), and suggested that the normal habitat of skipjack tuna is the lower salinity water which overrides the shallow salinity maximum.

Seckel (1972) observed that skipjack tuna landings in the Hawaiian skipjack tuna fishery were high in those years when initial warming of the water occurred before the end of February and the mean monthly salinity during spring was between 34.6 and 34.8‰, the latter value indicating the northern boundary of the California Current Extension water. Yasui and Inoue (1977) also noted good to excellent fishing off southern Japan in those years when the mean surface salinity was 34.81‰ and the mean surface temperature was 21.2°C. In poor years the mean salinity was 34.87‰ and the mean temperature was 19.8°C. In both instances, good fishing was related to favorable salinities, as well as favorable water temperatures.

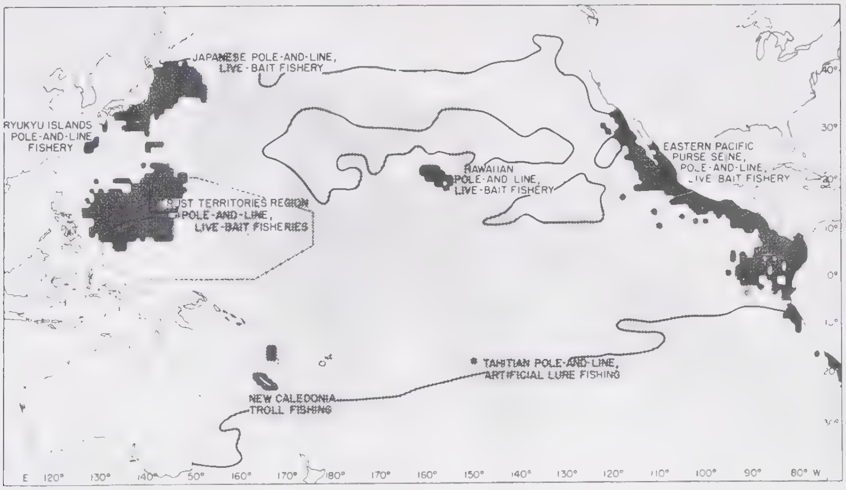

Figure 17.—Distribution of skipjack tuna in the Pacific Ocean (after Rothschild and Uchida 1968). The contours mark the boundaries of the area where a shallow subsurface salinity maximum is present either seasonally or permanently (from Barkley 1969).

Donguy et al. (1978), in comparing charts of skipjack tuna catches by the Japanese in the western Pacific for the period 1974-76 and surface salinity charts for 1957-75, noted that the catches of skipjack tuna were greater in waters with salinities of 35‰ or less in the area east of Papua New Guinea. In this instance the 35‰ isohaline in the region was found to be associated with the presence of a convergence.

(3) Surface currents

The circulation features of the major currents in both the Pacific and Atlantic Oceans, described previously in connection with distribution of larvae, also affect the distribution of adults. The flow toward the Equator of cool water on the eastern side of the oceans tends to restrict the distribution of fish in that region, and the poleward flow at the western side of the oceans permits a broader distribution there.

Surface currents affect the distribution of skipjack tuna in other ways. In currents flowing meridionally, tuna are considered to be distributed along the axis of the current and in greater abundance than in adjacent waters (Blackburn 1965). Such a relation was noted by Kawasaki (1958) and Uda (1962a) in the Kuroshio (warm current from the south) off Japan. Uda observed that more skipjack tuna became available to the fishery when the warm Kuroshio water extended over a broad area; and conversely, that a strong Oyashio (cold current from the north) hindered the movement of fish and catches were low.

Other effects of currents on the movement of fish have been indicated in the models of migration of skipjack tuna proposed by Seckel (1972), Williams (1972), Matsumoto (1975), and others. These migration models are described in Section 3.51.

(4) Hydrographic features

Fish tend to aggregate in areas where warm and cold water intrusions are well developed, in eddies, in areas of turbulent mixing, in oceanic fronts, convergences, upwelling, and other hydrographic features (Uda 1961, 1962b). Kawasaki (1958) noted that skipjack tuna fishing grounds developed off Japan when the warm Kuroshio water spread thinly over colder water and when the Kuroshio meandered in a complicated pattern. Uda (1962a) reported that good catches were also made when both the Kuroshio and the cold Oyashio currents were strong, under which conditions the skipjack tuna were concentrated along the boundary between the warm and cold water (polar front). Uda (1962b) further reported that in the eddies associated with the polar front, skipjack tuna were found in the warmer anticyclonic eddies along the front. Donguy et al. (1978) showed that skipjack tuna catches by the Japanese in the western Pacific, east of Papua New Guinea, were concentrated along and on the low salinity side of convergences (Fig. 18). Forsbergh (1969) reported that a marked salinity front was found at all seasons in the Panama Bight and that the abundance of skipjack (and yellowfin) tuna in the northern part of the Bight appeared to be related to the seasonal cycle of upwelling.

(5) Vertical distribution

Based on studies of tuna longline catches, Yabe et al. (1963) indicated that tunas are distributed by depth layers with the skipjack tuna occupying the shallowest layer, followed in order by the bluefin tuna, *Thunnus thynnus*; yellowfin tuna; bigeye tuna, *T. obesus*; and the albacore, *T. alalunga*. Skipjack tuna were assumed to occupy the shallowest depth layer largely on the basis that they are taken in commercial quantities almost entirely by fishing gear that require the fish to be at or very near the surface, and that the skipjack tuna are taken only incidentally on the deep-fishing longline.

Results from the use of echo sounders and underwater observations from small submarines have shown that the skipjack tuna not only occur over a much greater depth range than previously realized, but also in depths occupied by other tunas. Kimura et al. (1952) and Yamanaka et al. (1966) observed fish schools at depths of 140 and 120 m, respectively, which they identified as skipjack tuna when the schools subsequently rose to the surface. Strasburg et al. (1968) encountered skipjack tuna schools at depths of 98 to 152 m in Hawaiian waters during their numerous dives in a submarine. Tracking skipjack tuna tagged with ultrasonic transmitters in Hawaiian waters (Dizon et al. 1978) indicated that this species spends its time between the surface and 263 m during the day, but remains near the surface (within 75 m) at night. These depths are well within the depth range in which the yellowfin tuna are usually caught by longline.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

The skipjack tuna is normally heterosexual; however, a few instances of hermaphroditism have been recorded (Nakamura 1935; Raju 1960; Uchida 1961; Thomas and Raju 1964). In the two specimens described by Uchida from Hawaiian waters, the left and right gonads of one fish (Fig. 19) and the left gonad of the second fish were divided into three segments: an anterior ovarian section, a middle testicular section, and a posterior ovarian section; whereas the right gonad of the second fish was divided into two segments: an anterior two-thirds testicular section and a posterior one-third ovarian section. In both fish the anterior ovarian sections contained ripe resorbing ova but not in the posterior ovarian sections, a condition that could result from extrusion of ova from the latter during spawning but not from the former, due to the lack of an adequate oviduct. The testicular portions contained no running milt, but were described as well developed. Based on the developmental stages of the ovarian and testicular sections, Uchida believed that both fish were functional males and females.

3.12 Maturity

The minimum size of skipjack tuna at first spawning has not been defined, but a reasonable estimate can be made from the various published reports of fish with mature, ripe and spent ovaries, and of fish with ova diameters approaching 1.0 mm.

In the Pacific Ocean, Marr (1948) recorded skipjack tuna as small as 40 cm fork length (FL) with spent ovaries from

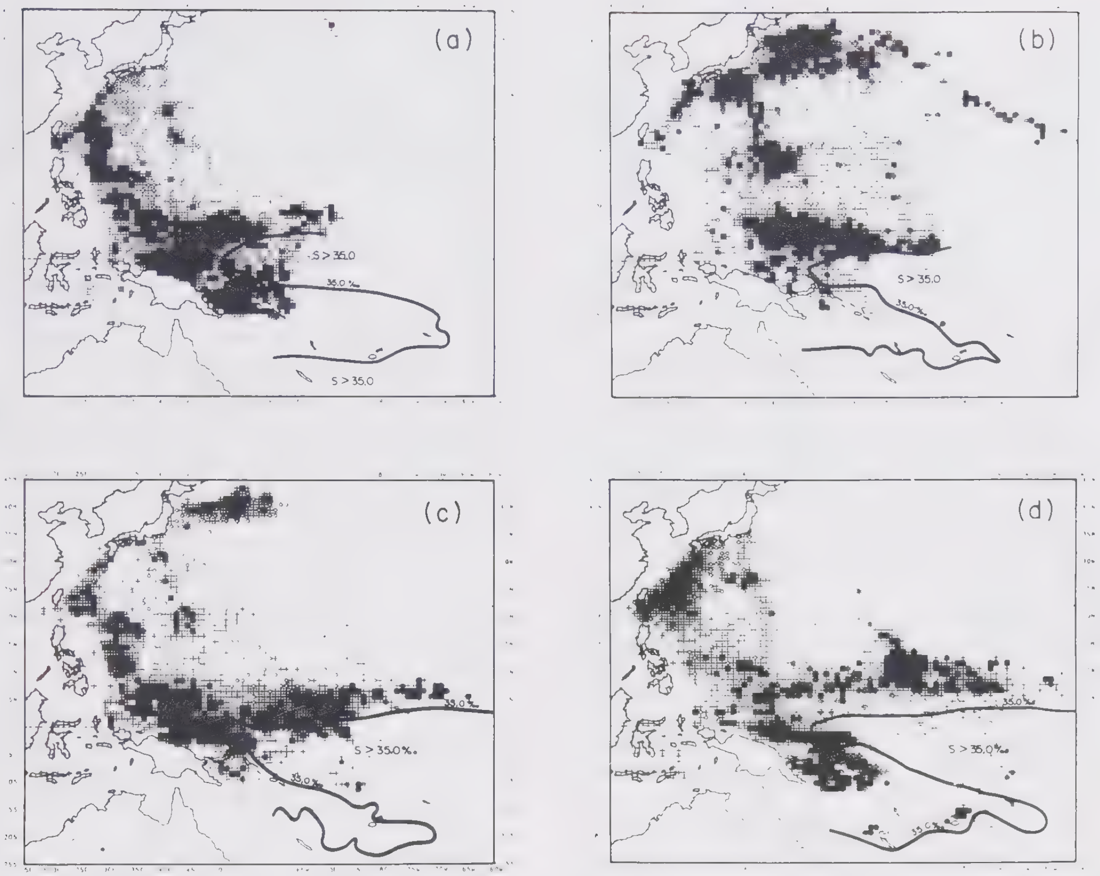

Figure 18.—Distribution of skipjack tuna catches and surface salinity in the western Pacific: a) January-March 1974, b) July-September 1974, c) October-December 1974, and d) January-March 1975. No catch denoted by 0, catches by +, and dark squares represent >700 t (from Donguy et al. 1978).

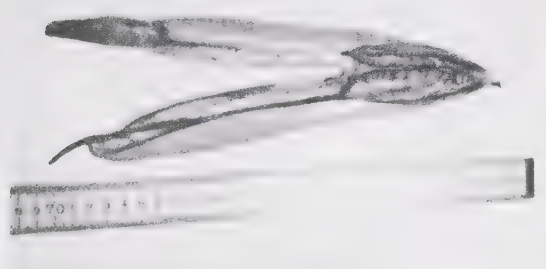

Figure 19.—Ovotestes of a hermaphroditic skipjack tuna (from Uchida 1961).

the Marshall Islands; Wade (1950) recorded fish in the 40.0 to 40.9 cm size class with ripe and spent ovaries from Philippine waters, and reported the capture of a female in the 34.0 to 34.9 cm size class having ripe ovaries; and Brock (1954) noted that the smallest fish that possessed maturing ova during the spawning season in Hawaiian waters were around 40 to 45 cm. Raju (1964c) estimated the size of sexual maturity of skipjack tuna in the Indian Ocean around Minicoy Island as about 40 to 45 cm. He derived his estimate from his observations that 1) the smallest skipjack tuna that possessed ovaries with maturing ova during the spawning season was around 40 to 45 cm and 2) remnants of mature ova were present in fish above 40 cm but none in fish below this size. Stequert (1976) reported first spawning of skipjack tuna at 41 to 43 cm off the northwest coast of Madagascar. Simmons (1969) reported minimum size of females at maturity in the Atlantic Ocean as 41 cm, as determined from fish with spawned or spent ovaries.

From the above, it appears that the minimum size of female skipjack tuna at maturity is 40 cm and that initial spawning can occur in fish between 40 and 45 cm or larger. The unusually small female (34.0-34.9 cm size class) with ripe ovaries reported by Wade (1950) could be a rarity or a case of erroneous staging of the gonads (see Section 3.15 for discussion of maturity stages of gonads).

3.13 and 3.14 Mating and fertilization

Iversen et al. (1970) observed what they believed to be courtship of skipjack tuna from an underwater sled towed from the RV *Charles H. Gilbert*. While observing a pair of skipjack tuna approximately 50 cm long, swimming close together back and forth in front of the sled, they noticed that the fish's bodies would tilt about 30° from the vertical in opposite directions with the ventral portions of their bodies almost touching each other. At another time they saw two fish swimming in tandem, one ahead of the other. The latter fish, situated slightly below the lead fish, would approach it closely from the rear, its snout coming within a few centimeters of the caudal fin of the lead fish. At the closest point of approach, the trailing fish would display dark vertical bars on its side, similar to that displayed during feeding. A second pair of skipjack tuna swimming in tandem were observed from the deck of the vessel. On two occasions the lead fish was seen to wobble from side to side and the trailing fish would exhibit vertical bars along its flanks. These fish showed no interest in the baitfish thrown into the water, so that the appearance of the bars were not likely connected with feeding (see Section 3.41 on feeding behavior).

Observations of similar behavior, believed to be mating or courting acts, have been observed by longtime skipjack tuna fishermen (e.g., R. M. Oka[6]) in the Hawaiian Islands. Schools of fish displaying such behavior were reported to be reddish- or purplish-hued and as being disinterested in feeding. The senior author has observed similar schools on several occasions and when the visibility, sea, and light conditions were right, whitish trails of spawn could be seen at the point of contact when two fish came together. The contacts seemed to occur randomly throughout the rapidly moving schools.

These observations suggest that mating is most likely promiscuous, and other observations such as the collection of eggs in various stages of embryonic development in plankton nets suggest that fertilization occurs externally.

3.15 Gonads

In the early years, sexual maturity of the skipjack tuna was determined by the general appearance of the gonad (Matsui 1942; Marr 1948; Yao 1955; Williams 1964). The characters most used were size of gonad and degree of softness or turgidity. Others (Buñag 1956; Raju 1964c; Kawasaki 1965a) felt that these general characters alone were inadequate even for gross classification. Some improvements were made by including the description of ova in the various stages of development (Buñag 1956; Schaefer and Orange 1956; Raju 1964c; Yoshida 1966; Simmons 1969; Batts 1972c), but the classification still remained subjective and was prone to variations caused by the observer's interpretation of the various stages.

Buñag (1956) and Raju (1964c) classified sexual maturity on the basis of ovum diameter measurements. Yoshida (1966) and Batts (1972c) provided ovum diameter measurements along with descriptions of ova, ovaries, or both. Yet the classification by these authors differed noticeably, since a standard scale defining the various stages of development had not been established for tunas. Buñag (1956) attempted to classify the stages according to the International Maturity Scale,[7] but no one else has followed his example. A summary of the maturity stages of female skipjack tuna based on ova diameter and descriptions of ova and ovaries from the preceding studies is presented in Table 5.

To avoid measuring ova, some authors have used gonad indices (G.I.) to determine maturity (Yabe 1954; Schaefer and Orange 1965; Orange 1961; Raju 1964c; Yoshida 1966; Batts 1972c). Schaefer and Orange (1956) obtained a linear relationship between ovum diameter and G.I. (Fig. 20) of fish taken in the eastern tropical Pacific. They thus concluded that maturity of female skipjack tuna could be determined on the basis of G.I. values. Their data, however, consisted mainly of G.I. below 50 from samples that included only few fish larger than 60 cm. Raju (1964c) also obtained similar results (Fig. 21) from fish taken off Minicoy Island in the Indian Ocean; however, his sample included larger fish and the largest G.I. was about 66.

Yoshida (1966), whose study was based on fish from the Marquesas and Tuamotu Islands in the central Pacific, reported G.I. values ranging from 20 to over 90 for ovaries in the developing stage (ovum diameters 0.5 to 0.6 mm) and from 30 to nearly 100 for ovaries in the advanced stage (ovum diameters 0.6 to 0.7 mm). He noted that there was a large overlap in the G.I. values between these two stages and that the linear relationship reported by Schaefer and Orange

Table 5.—Summary of maturity stages of female skipjack tuna.

Stage	Designation	Largest ova diameter (mm)	Description of ova	Description of ovary
I	Immature	0.15	Ova transparent; with nucleus	Slender, elongate; sex determinable
II	Early maturing	0.35	Ova opaque; yolk forming	Enlarged; ova not visible
III	Late maturing	0.60	Ova opaque; yolk granular	Enlarged, turgid; ova visible
IV	Mature	0.85	Ova transparent; with oil cluster or oil droplet	Enlarged, begin losing turgidity; ova visible, easily dislodged
V	Ripe	1.00	Ova with yellow oil droplet	Greatly enlarged, not turgid; ova easily dislodged, some free in lumen; extruded by pressure
VI	Spent	0.55	Ova remnants 1.0 mm	Flaccid, with remnants of ripe ova

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[6] R.M. Oka, formerly commercial skipjack tuna pole-and-line fisherman and leading fisherman on the RV *Charles H. Gilbert*, pers. commun. June 1969.

[7] Maturity scale adopted by the International Council for the Exploration of the Sea, as cited by Clark (1934).

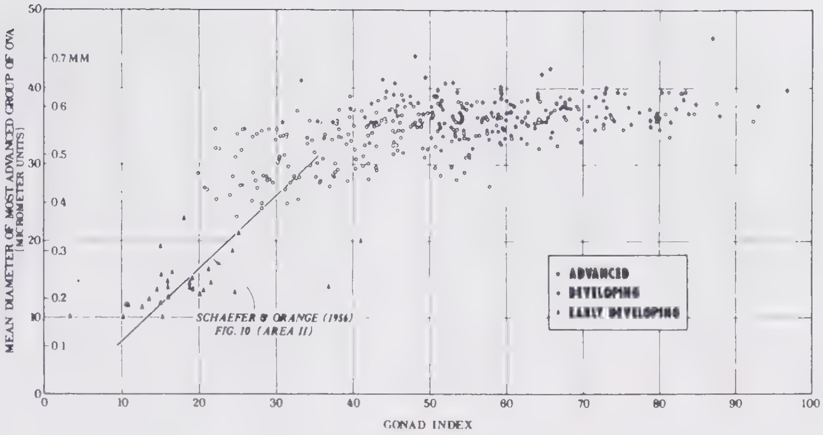


Figure 20.—Relationship between gonad index (ovary weight relative to fish length³) and mean diameter of most advanced group of ova of skipjack tuna from the Marquesas and Tuamotu Islands (from Yoshida 1966).

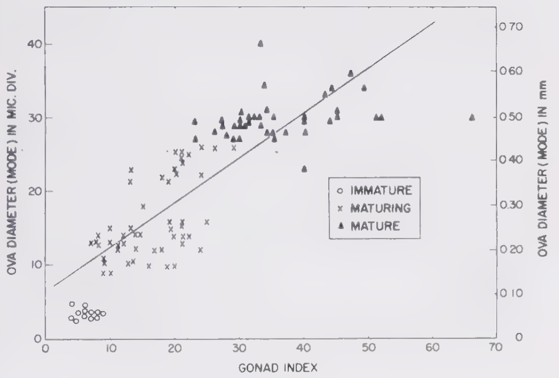


Figure 21.—Relationship between gonad index (ovary weight relative to fish length³) and modal length of largest group of ova of skipjack tuna from Minicoy (from Raju 1964c).

(1956) was not applicable to G.I. values above 36 (Fig. 20). We should also add that the linear relationship shown by Raju (1964c) in Figure 21 does not seem valid either. Because of the wide range of G.I. values for ovaries in the same developmental stage, the gonad index does not seem to be a sound measure of maturity for skipjack tuna.

3.16 Spawning

(1) Fecundity

Relatively little has been published concerning the fecundity of skipjack tuna. The fecundity range has been reported as 100,000 to 2 million ova for fish 43.0 to 87.0 cm long from the Pacific Ocean, 87,600 to 1,977,000 ova for fish 41.3 to 70.3 cm long from the Indian Ocean, and 141,000 to 1,331,000 ova for fish 46.5 to 80.9 cm long from the Atlantic Ocean (Table 6). Plots of number of ova in the most advanced mode against fish size by Joseph (1963), Raju (1964a), Sim-

Table 6.—Observed fecundity estimates for skipjack tuna.

Source of data	Locality	Number of fish	Fish length (range) (mm)	Estimated ova (range)
Pacific Ocean				
Yabe (1954)	Ryukyu Islands	5	468-610	113,364-859,897
Rothschild (1963)	Hawaiian Islands	3	440-870	280,000-1,900,000
Joseph (1963)	Eastern Pacific	42	614-715	210,000-1,490,000
Yoshida (1966)	Marquesas Islands	4	430-750	100,000-2,000,000
Indian Ocean				
Raju (1964a)	Minicoy Island	63	418-703	151,900-1,977,900
Stequert (1976)	Madagascar	64	441-565	87,600-824,000
Atlantic Ocean				
Simmons (1969)	Caribbean Sea	13	465-809	262,000-1,331,000
Batts (1972c)	North Carolina, U.S.A.	31	498-704	141,000-1,200,000

mons (1969), and Batts (1972c) show considerable variation among fish of the same size. All four authors fitted regression lines to the relationship between fecundity and length (Table 7; Fig. 22), but due either to inadequate sample size or to samples of limited size ranges, the regression lines varied noticeably. Raju (1964a) fitted regression lines also to the relationship between fecundity and the square of the fish length, and both he and Simmons (1969) fitted regression lines to the relationship between fecundity and the cube of the length. The latter regressions had the higher coefficients of correlation, although all four regressions were statistically significant ($P = 0.01$). Joseph (1963) and Raju (1964a) fitted regression lines to the relationship between fecundity and fish weight also. Both reported smaller standard error of estimates than those obtained from any of the fecundity-length relationships, whereas the latter obtained a coefficient of correlation only slightly higher than that of the fecundity-length cubed relationship. The closeness of the coefficients of correlation is understandable, since weight is nearly proportional to the cube of the length for skipjack tuna. Consequently, either the length cubed or weight may be used to describe the relationship between fecundity and fish size.

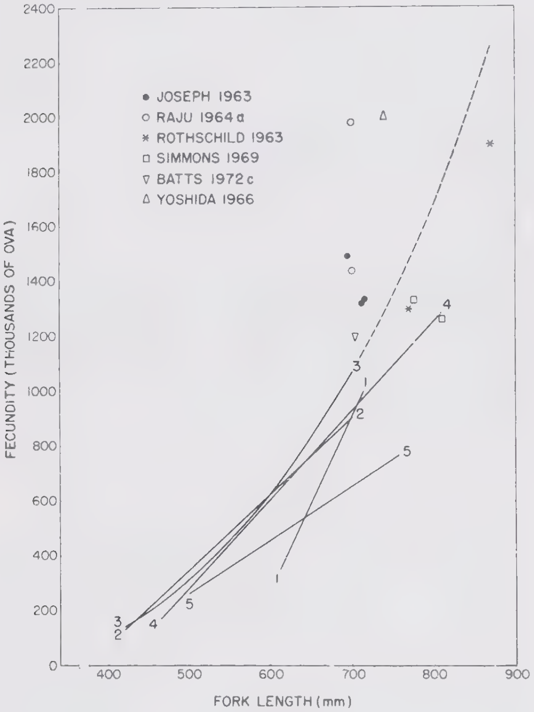


Figure 22.—Regressions of fecundity on length and observed fecundity estimates of skipjack tuna above 690 mm. 1) Joseph (1963); 2) Raju (1964a); 3) fecundity-length^3, Raju (1964a); 4) Simmons (1969); and 5) Batts (1972c).

Using Raju's (1964a) fecundity-length cubed relationship, the calculated fecundity estimate of skipjack tuna at minimum spawning size (40.0 cm) is 110,000 ova. That Raju's fecundity-length cubed relationship holds reasonably well for fish larger than about 69.0 mm is noted in Figure 22, which shows the extension of the curve and also the observed fecundity of fish above this size by various authors.

In spite of the acceptable fecundity-length cubed relationship noted above, it would be most difficult to estimate the total annual egg production of the skipjack tuna because of 1) the extremely large variation in number of ova among fish of the same size, 2) the uncertainty in the number of times a fish spawns during the year (Section 3.16), 3) the possibility of reduced fecundity at successive spawnings in the same year (Joseph 1963), and 4) incomplete knowledge concerning the size composition and total abundance of the spawning stocks.

(2) Frequency

The possibility of skipjack tuna spawning more than once during a season has been discussed by several authors. Brock (1954) was of the opinion that the multimodal distribution of ovum diameters during the spawning season and its absence at other times indicated that individual skipjack tuna taken in Hawaiian waters spawn several times. As supporting evidence, he cited the absence of an overall trend in ovum diameters during the spawning season (Fig. 23) and the absence of spawned-out fish until after the end of the spawning season. Buñag (1956) determined multiple spawning by following the movement of ovum diameter modes through the various stages of development as indicated by ovum diameter frequency plots (Fig. 24). Raju (1964c) determined multiple spawning from the Indian Ocean by satisfying the four lines of evidence used by Clark (1934): 1) The presence of multiple modes in diameter frequency polygons, 2) obtaining a high correlation in the progression of successive modes, 3) the

Table 7.—Comparison of fecundity-length and fecundity-weight relationships of skipjack tuna from various sources.

Source	Relationship	*a* (thousands)	*b*	Standard error of estimate (thousands)		*P*
Joseph (1963)	[1]$Y = a + bL$ (1)	$-3,503$	6.326	276	—	—
	$Y = a + bW$	-608.807	88.613	273	—	—
Raju (1964a)	$Y = a + bL$ (2)	$-1,004.94$	2.713	28.6	0.645	≤ 0.01
	$Y = a + bL^2$	-292.26	0.00254	27.4	0.668	≤ 0.01
	[1]$Y = a + bL^3$ (3)	-109.0	0.00000342	24.7	0.741	≤ 0.01
	$Y = a + bW$	-67.69	67.01	22.5	0.789	≤ 0.01
Simmons (1969)	[1]$Y = a + bL$ (4)	$-1,333.541$	3.238	—	0.873	≤ 0.01
	$Y = a + bL^3$	—	—	—	0.886	≤ 0.01
Batts (1972c)	[1]$Y = a + bL$ (5)	-632.085	1.854	—	—	—

Number in parentheses refers to regression line in Figure 22.

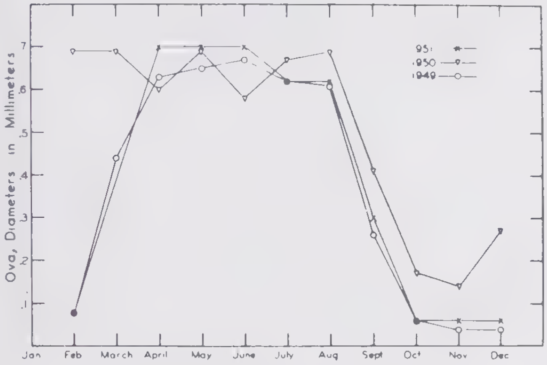


Figure 23.—Average modal diameter of the largest group of ova in skipjack tuna ovary samples collected from 1949 to 1951 in Hawaiian waters (from Brock 1954).

presence of ova remnants in maturing ovaries, and 4) the decrease in the numerical ratio of ova between maturing and mature group.

From the results of these studies, there seems to be little doubt that skipjack tuna spawns more than once during a season. How many times it spawns is not yet known, but utilizing the reports by Brock (1954) and Buñag (1956), the number of spawnings can be estimated, at least for fish in Hawaiian waters.

From Brock's 1949 and 1951 data in Figure 23, we note that in Hawaiian waters, fish with immature ova (ova diameter 0.1 mm) occurred in February, and in 2 mo the ova developed into the mature stage (ova diameter 0.7 mm). If development continues at this same pace, the ova should be in the ripe stage (Yabe 1954; Yoshida 1966; Batts 1972c) with diameters from 0.8 to 1.2 mm in late April or early May. This is supported by the first captures of larval skipjack tuna in Hawaiian waters in late April and early May (Seckel 1972). Buñag (1956), as well as others, had observed that after the first batch of ripe ova has been spawned, the ovaries revert to the condition similar to that of ovaries in maturity stage III (Fig. 24), i.e., ova in the most advanced group are not much larger than about 0.58 mm (18 micrometer units). Ova of this size would require about 6-7 wk to reach the ripe stage (based on Brock's data), exclusive of a probable resting period after the initial spawning. Hence, the earliest that a skipjack tuna could spawn a second time after having spawned once in early May would be in late July or early August. Since the spawning season in Hawaiian waters terminates in September (Brock 1954), it would be unlikely for this species to spawn a third time in the area. This does not mean that a third or even a fourth spawning could not occur. In fish with ovaries developing more than two groups of ova, migration to warmer waters in the fall and winter could allow it to spawn a third or even a fourth time during a year.

Another bit of information may be gleaned from Figure 23. If the first spawning occurs as described, then the duration of ova development from the immature to the ripe or spawning stage can be estimated as being from 3 to 3.5 mo.

(3) Spawning in captivity

Current interest in mariculture has resulted in many attempts to rear tunas in captivity. Collection of ripe ova from females at sea has only resulted in sporadic success, probably due to the paucity of running ripe females in the commercial catches and because attempts to hold adults as brood stock has proven inefficient and costly.

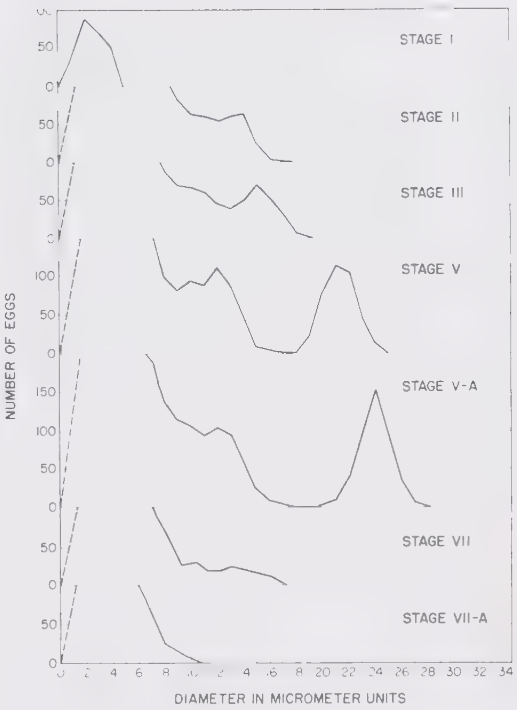


Figure 24.—Ova diameter frequency polygons of skipjack tuna with the stages of ova development (from Buñag 1956). [Each micrometer unit equals 0.0325 mm.]

In June and July of 1980, female skipjack tuna (1.4-2.2 kg) confined at the Kewalo Research Facility of the U.S. National Marine Fisheries Service in Honolulu ovulated ripe ova within 8 h after capture (Kaya et al. 1982). The rapid development of the ova, followed by ovulation and spawning, apparently was induced by stresses experienced by the fish during capture and confinement. The ripe ova measured approximately 1.0 mm as compared with unovulated ova, 0.59-0.74 mm, obtained from fish taken from the same school and iced immediately upon capture. Artificial fertilization of the ripe ova resulted in successful embryonic developement and subsequent hatching of the larvae. Males brought live to the holding tanks did not respond in the same manner. Their testes were identical to those of fish iced immediately upon capture. Although all testes were mature, they failed to yield milt on moderate stripping pressure. Small amounts of thick milt obtained from excised testes, however, were successfully used in fertilizing the ripe ova stripped from captive females.

The rapid maturation and ovulation processes brought on by capture and confinement stresses are currently being exploited to routinely produce larval skipjack tunas for developmental and growth studies at the Kewalo Research Facility.

(4) Areas and seasons

Gonadal studies in the Pacific, Atlantic, and Indian Oceans indicate that skipjack tuna spawn throughout the year in tropical waters near the Equator and from spring to early fall in subtropical waters, with the spawning period becoming shorter as distance from the Equator increases. Because sampling for gonads requires the capture of adults, these studies have generally been restricted to specific areas where fishing has been done on a commerical basis or in areas subjected to heavy experimental fishing. Such areas include waters south of Japan, Philippines, Marshall Islands, Hawaiian Islands, New Caledonia, Marquesas-Tuamoto Archipelago, and off Central America in the Pacific Ocean (Kishinouye 1923; Marr 1948; Wade 1950; Brock 1954; Yabe 1954; Yao 1955; Schaefer and Orange 1956; Orange 1961; Yoshida 1966; Legand 1971; Naganuma 1979); waters off Ghana, Ivory Coast, Sierra Leone, Cape Verde Islands, Lesser Antilles, Cuba, and North Carolina in the Atlantic Ocean (Rivero and Fernandez 1954; Frade and Postel 1955, Gorbunova and Salabarría 1967; Simmons 1969; Zhudova 1969; Batts 1972c); and waters around Madagascar, Minicoy Island, and throughout the tropical zone in the Indian Ocean (Raju 1964c; Marcille and Suzuki 1974; Stequert 1976).

Larval captures, also indicative of spawning activity, have occurred not only in the areas mentioned above and in similar months, but also in intervening waters, e.g., Pacific Ocean—Matsumoto (1958), Strasburg (1960), Klawe (1963), Nakamura and Matsumoto (1967), Ueyanagi (1969, 1970); Atlantic Ocean—Richards (1969), Richards and Simmons (1971), Ueyanagi (1971); Indian Ocean—Jones (1959), Gorbunova (1963, 1965a), Jones and Kumaran (1963), Ueyanagi (1969).

3.17 Spawn

Ripe ovarian eggs are spherical, smooth, transparent, and usually contain a single yellow oil droplet (Brock 1954; Yabe 1954; Yoshida 1966). Eggs are 0.80 to 1.17 mm in diameter, with mean diameters ranging from 0.96 to 1.135 mm. The oil droplet varies greatly in size: Yabe (1954) reported a range of 0.22 to 0.27 mm, Brock (1954) gave a range of 0.22 to 0.45 mm, and Yoshida (1966) reported an average of 0.14 mm. That eggs of this size range are fully ripe and capable of being fertilized has been shown by Ueyanagi et al. (1973, 1974) and Kaya et al. (1982).

Eggs of other species of scombrids that have been fertilized artificially (frigate tuna, *Auxis thazard*; bullet tuna, *A. rochei*; and yellowfin tuna) and reared through the hatching stage are comparable in size and appearance with those of skipjack tuna (Harada et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973; Ueyanagi et al. 1973). Consequently, tuna eggs collected at sea in plankton nets are extremely difficult to identify to species.

The spawned eggs of tunas are buoyant in nature (Kikawa 1953; Harada et al. 1971; Harada, Murata, and Furutani 1973; Harada, Murata, and Miyashita 1973). During experiments in rearing artificially fertilized yellowfin tuna eggs, Kikawa (1953) observed that most of the eggs which were presumably dead turned opaque and sank to the bottom, but those still viable were transparent and buoyant. The opaque eggs were found to be in arrested stages of cleavage, whereas the buoyant eggs contained developing embryos.

3.2 Preadult phase

3.21 Embryonic phase

Development of the skipjack tuna embryo has been studied in detail by Ueyanagi et al. (1973, 1974) from artifically fertilized eggs. They noted that embryonic development proceeded rapidly after fertilization (Fig. 25) and the larvae hatched in about 1 d. The incubational period noted by the former authors was 26 to 31 h in 23° to 25°C water, 21 to 32 h in 24.2° to 27°C water, and 21 to 22 h in 26° to 29°C water; whereas, the latter reported 22 to 27 h in 27°C water. Hence, there is some indication that incubational period is related inversely to water temperature.

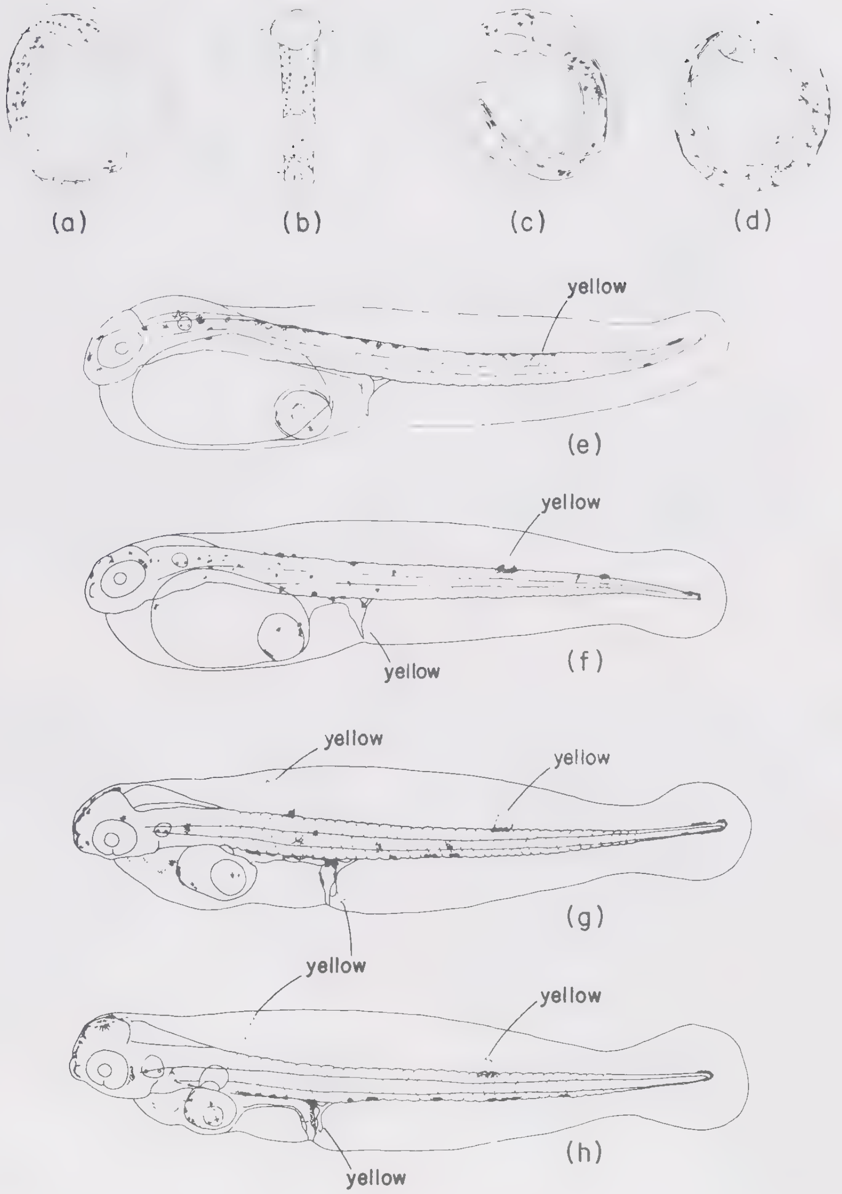
3.22 Larval phase

Total length (TL) is used in discussing tuna larvae. It represents the distance from the snout to the end of the longest caudal ray before the caudal fin has forked. On larger larvae total length equals fork length.

The newly hatched larva (Fig. 25) is about 2.6 mm TL (Ueyanagi et al. 1974), comparable with the size estimated by Matsumoto (1958). According to Ueyanagi et al., the larvae absorbed their yolk sac within 2 d after hatching, but due to unsuccessful initial feeding, they died within 5 d.

The development of the larvae is shown in Figures 25 and 26. Ueyanagi et al. (1974) described the earliest stages of the larvae thus: "Yellow pigment spots on the finfold were conspicuous in the prelarval stage. Small melanophores appeared on the dorsal edge of the trunk in the early prelarval stage and moved toward the ventral edge [where they] tended to converge toward the caudal peduncle." The convergence of these melanophores at the caudal peduncle leads to the eventual formation of a single, distinct black spot (Fig. 26a-d), one of the principal identifying characters of the skipjack tuna larva. Other characters describing the larvae have been reported in Wade (1951), Yabe (1955), Ishiyama and Okada (1957), and Matsumoto (1958). These include a disproportionately large head which is bent slightly downward in relation to the body axis, the appearance of 2 or 3 melanophores over the forebrain area when the larvae are about 7 mm long (the number of melanophores increases to about 12 in larvae about 14.5 mm in length), heavy pigmentation over the midbrain area throughout all sizes, and the appearance of the first dorsal fin spines in larvae about 7 mm long (the number of spines increases to about 13 in larvae 11 mm TL). Pigmentation on the first dorsal fin is limited to scattered melanophores near the outer edge of the fin (Fig. 26d). The full complement of 16 spines and 15 rays in the first and second dorsal fins, respectively, and 15 rays in the anal fin are developed by the time the larvae are about 12 mm long. At this stage the young are considered as juveniles.

The juvenile stage is characterized by a more fusiform body and by a general increase in pigmentation over all parts of the body. Juveniles up to 47 mm (Fig. 27d) are easily identified by the concave outline of the first dorsal fin and its characteristic pigmentation, the moderately long snout, and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(b)
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Figure 25.—Development of eggs and prelarval stage of skipjack tuna. a) 12 h after fertilization, 1.01 mm in diameter; b) 15 h, 1.00 mm; c) 22 h, 0.97 mm; d) 23 h, 0.99 mm; e) just after hatching, TL 2.65 mm; f) 4 h, after hatching, TL 2.96 mm; g) 10 h, TL 3.30 mm; h) 19 h, TL 3.36 mm; i) 33 h, TL 3.57 mm; j) 43 h, TL 3.70 mm; k) 84 h, TL 3.55 mm (from Ueyanagi et al. 1974).

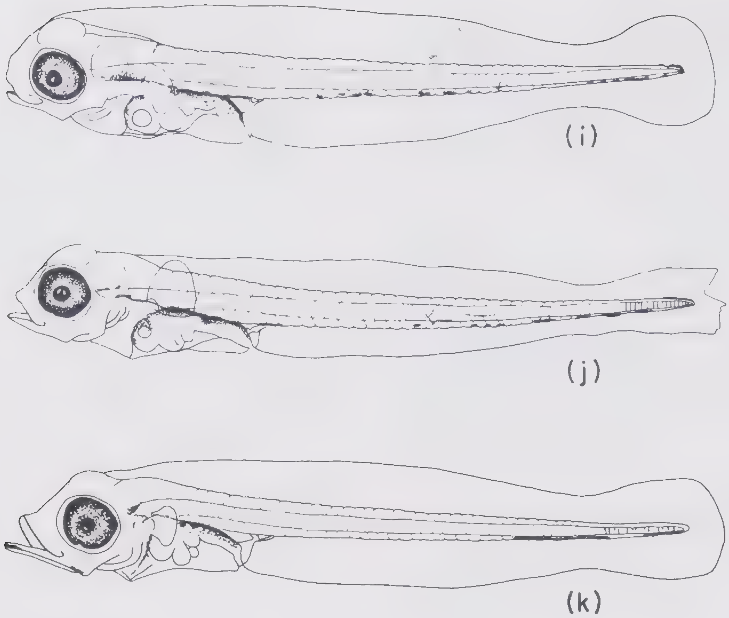

Figure 25.—*Continued.*

the number of vertebrae (20 precaudal and 21 caudal). The first dorsal fin has scattered melanophores on the first three or four interspinal membranes and along the distal edge of the remaining membranes. The only other genus in which the juveniles are known to have similar-shaped first dorsal fins is *Euthynnus* (Schaefer and Marr 1948; Wade 1950; Mead 1951). In *Euthynnus*, however, the first dorsal fin is either completely or almost completely pigmented. Also, unlike *Euthynnus*, juveniles of skipjack tuna do not develop dark vertical bands over the dorsal half of the body.

According to Godsil and Byers (1944) and Godsil (1954), adult skipjack tuna lack a swim bladder. Richards and Dove (1971), however, reported that all tuna larvae, including larvae of the skipjack tuna, develop swim bladders and gas glands at the smallest sizes studied (2.6 mm standard length), but that the swim bladder degenerates in skipjack tuna before the fish reaches a size of 20 mm. According to these authors, degeneration of the swim bladder begins when the larvae reach a size of 9.0 mm and the swim bladder is nearly absent in specimens 24.0 mm long. Only the gas gland remains in juveniles above this size.

3.23 Adolescent phase

Juveniles below the size of first spawning (ca. 40 cm) have not been described and there is no information in the literature describing the initial appearance of the longitudinal black stripes along the sides of the body below the lateral line.

3.3 Adult phase

3.31 Maximum size and longevity

It is common practice to fit a von Bertalanffy or negative exponential curve to a set of size data and report the estimate of L_∞ thus obtained as the maximum size of a fish. It should be remembered that L_∞ is a parameter mathematically characterizing the asymptotic phenomenon we call maximum size of a fish. Our estimate of it is a statistic whose accuracy is dependent upon the representativeness of the sample used in the calculation, and whose variance is, among other things, dependent upon the sample size. Thus if we need an estimate of maximum size for other model building, e.g., estimating sustainable yield, then a statistic is what is needed. If we want to describe the maximum size of a fish, then it may suffice to report the largest fish recorded to date. In the following paragraphs we will follow the latter procedure, while later in Section 3.43, we will present estimates of L_∞.

Miyake (1968) listed a skipjack tuna in the 106.5 to 108.4 cm size class taken on tuna longline. Although he made no reference to this fish, it could well be the largest skipjack tuna ever recorded. A fish of this size class, using the length-weight relation developed for fish in the central North Pacific (Nakamura and Uchiyama 1966), would weigh between 32.5 and 34.5 kg (71.6 and 76.0 lb). On the basis of growth parameters computed from data on modal progression and otolith readings (Table 8), such a fish would have a minimum age of 8-12 yr.

3.32 Hardiness

As already discussed under Section 2.32, skipjack tuna can withstand a wide range of temperatures. At sea they have been found in water with temperatures as high as 30 °C and as low as 14.7 °C, which approaches the lower lethal ambient temperature of 13 °C, as proposed by Stevens and Fry (1971). However in the short term and locally, skipjack tuna inhabit epipelagic waters characterized by narrow variations in oceanographic features. (Additional discussion in Section 3.6.)

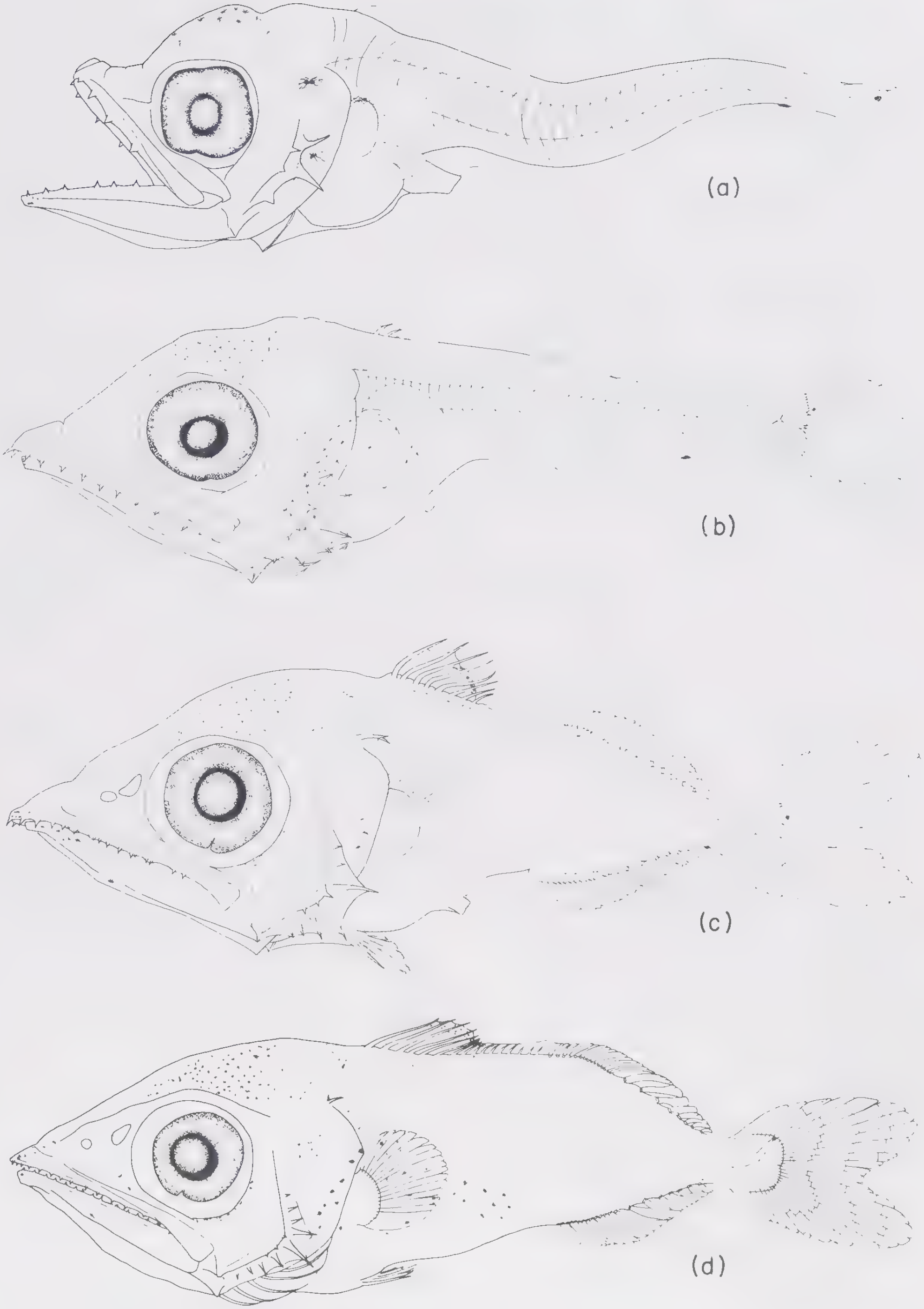

Figure 26.—Skipjack tuna larvae. a) 3.7 mm TL; b) 6.7 mm TL; c) 8.75 mm TL; d) 10.9 mm TL (from Matsumoto 1958).

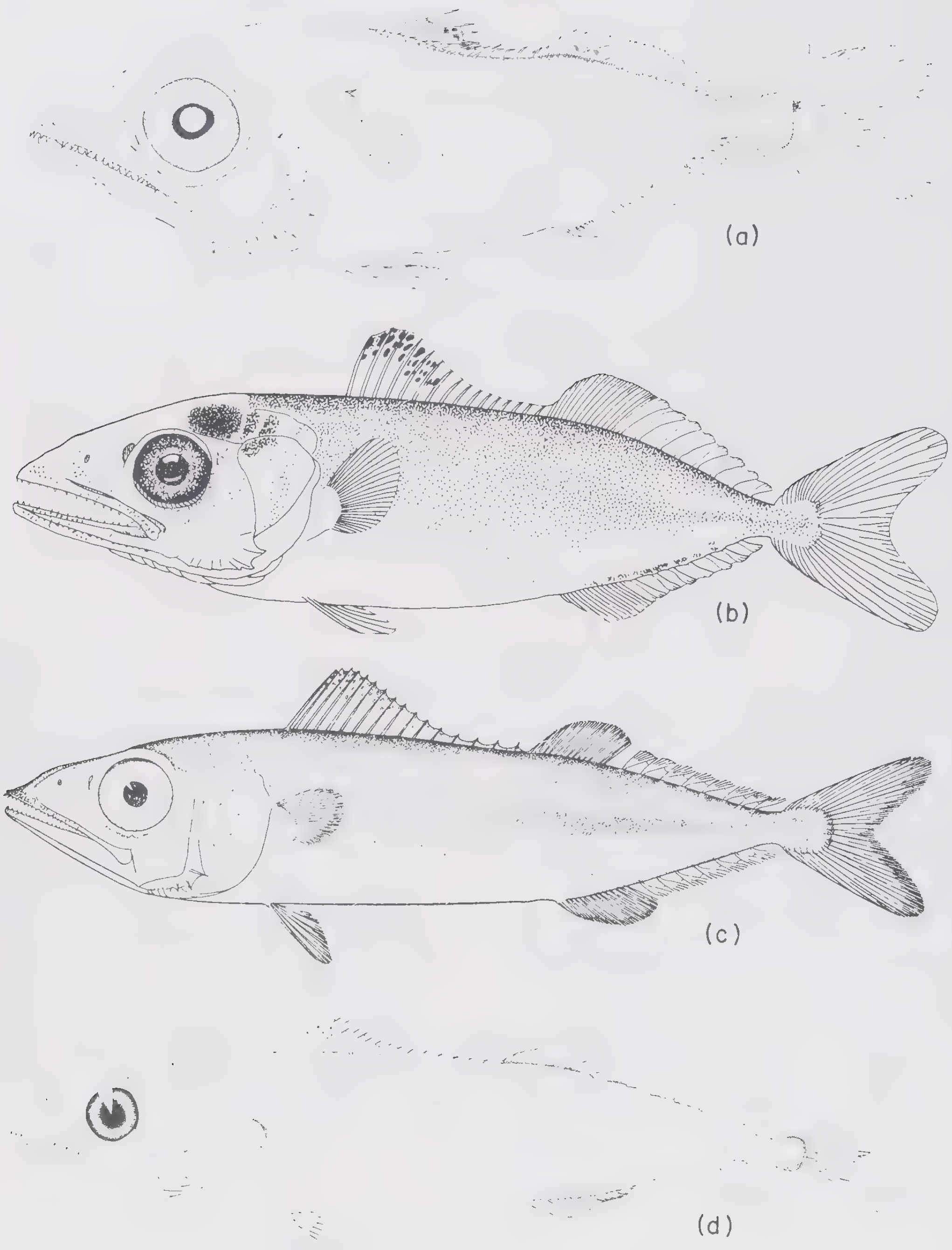

Figure 27.—Juvenile skipjack tuna. a) 14.5 mm TL; b) 21.0 mm TL; c) 27.0 mm TL; d) 47.0 mm TL (from Schaefer and Marr 1948; Wade 1950; Matsumoto 1958, 1961).

Table 8.—Size (fork length in centimeters) at age and growth parameters of skipjack tuna from the Pacific, Indian, and Atlantic Oceans.

		Age in years								Growth parameters			
Source	Area	0	1	2	3	4	5	6	7	t_0	K	l_{∞}(cm)	Method
Pacific Ocean													
Aikawa (1937)	East of Japan	<26	26	34	43	54	—	—	—	—	—	—	Vertebrae
Aikawa and Kato (1938)	Palau	<27	27	37	46	55	64	72	80	—	—	—	Vertebrae
Chi and Yang (1973)	Taiwan	<27	27	47	62	73	81	—	—	−0.016	0.302	103.6	Vertebrae
Yokota et al. (1961)	South of Japan-Sulu Sea	—	37	52	64	73	85	—	—	—	—	140.0	Modal analysis
Joseph and Calkins (1969)	East of Japan	0.3	25	45	62	75	—	—	—	—	0.19	141.8	Modal analysis; Kawasaki's (1963) data
Kawasaki (1965a)	South of Japan and Hawaii	—	15	45	63	73	77	—	—	—	—	—	Modal analysis
Chi and Yang (1973)	Taiwan	<36	36	60	75	—	—	—	—	−0.016	0.432	103.8	Modal analysis
Yoshida (1971)	Central Pacific	—	35	—	—	—	—	—	—	—	—	—	Modal analysis; juveniles
Uchiyama and Struhsaker (1981)	Hawaii	—	43	68	79	83	—	—	—	—	0.92	85.5	Modal analysis; Brock's (1954) data
Joseph and Calkins (1969)	Eastern Pacific	0.3	30	50	62	70	—	—	—	—	0.44	85.1	Modal analysis; Schaefer's (1961a) data
Joseph and Calkins (1969)	Eastern Pacific	0.3	37	60	76	87	—	—	—	—	0.41	107.5	Modal analysis
Joseph and Calkins (1969)	Hawaii	0.3	44	65	74	78	—	—	—	—	0.77	82.3	Tagging; corrected data from Rothschild (1967)
Joseph and Calkins (1969)	Hawaii	0.3	40	63	75	82	—	—	—	—	0.59	90.6	Tagging; uncorrected data from Rothschild (1967)
Skillman[1]	Hawaii	—	43	61	74	83	—	—	—	—	0.39	101.1	Tagging; males only
Skillman[1]	Hawaii	—	43	61	73	80	—	—	—	—	0.47	92.4	Tagging; males and females
Joseph and Calkins (1969)	Eastern Pacific	0.3	31	51	64	72	—	—	—	—	0.431	88.1	Tagging; averaged data
Joseph and Calkins (1969)	Eastern Pacific	0.3	41	59	67	70	—	—	—	—	0.829	72.9	Tagging; non-averaged data
Uchiyama and Struhsaker (1981)	Hawaii	—	44	68	83	91	—	—	—	−0.02	0.55	102.0	Otolith
Indian Ocean													
Shabotiniets (1968)	Indian Ocean	—	—	—	40-45	40-60	—	—	—	—	—	—	First dorsal spine
Atlantic Ocean													
Batts (1972a)	Western North Atlantic	—	41	49	57	64	—	—	—	−4.329	0.195	79.6	First dorsal spine

[1] See text footnote 10.

Under abnormal conditions, such as when fish are caught and handled for experimental purposes, skipjack tuna are not quite as hardy as other tunas and not nearly as hardy as some other marine or freshwater species commonly used in laboratory experiments. Skipjack tuna can be used as an experimental animal but laboratory procedures must be designed with care. Mark-recapture experiments have been conducted successfully, but the animals must be handled quickly and with care.

3.33 Competitors

Fish that have been observed or taken with feeding aggregations of skipjack tuna (Gudger 1941; Waldron 1963) have been considered as competitors of skipjack tuna. These fish include yellowfin tuna; albacore; kawakawa, *Euthynnus affinis*; frigate tuna; dolphin, *Coryphaena hippurus*; rainbow runner, *Elagatis bipinnulata*; and whale shark, *Rhineodon typus*.

In addition, seabirds may be considered as competitors, for both they and skipjack tuna feed on the same aggregations of forage fishes at the sea surface.

3.34 Predators

Predators of either juvenile or adult skipjack tuna are listed in Table 9.

3.35 Parasites, diseases, injuries, and abnormalities

Parasites found in skipjack tuna have been listed by Waldron (1963), Silas (1967), and Silas and Ummerkutty (1967). The list by Waldron includes 26 trematodes, 4 cestodes, 2 nematodes, 1 or more acanthocephalids, and 10 copepods; that by Silas includes 33 trematodes and 1 cestode; and that by Silas and Ummerkutty includes 10 copepods. The last two studies also provide information such as host, locality, location of infestation, and pertinent remarks on nomenclature or occurrence. Chen and Yang (1973) listed one species each of trematode, cestode, and nematode, and two species of acanthocephalids in skipjack tuna from waters off Taiwan. We have not seen the report by Love and Moser (1977), however, Forsbergh (1980) stated that these authors listed 36 species of trematodes, 1 specie of cestode, 12 species of copepods, and 6 species of nematodes and acanthocephalids. Cressy and Cressy (1980) presented a comprehensive account of copepods parasitic on tunas and tunalike fishes on a worldwide basis. Because of the unreliability of most past literature, they attempted to clarify the taxonomic status of both parasites and hosts. They resolved problems of synonymy of several species of copepods and listed five species parasitic on skipjack tuna which they had collected during the course of their study.

The list of parasites (Table 10) was compiled from the papers examined above.

Table 9.—Predators of either juvenile or adult skipjack tuna.

Predator	Source
Skipjack tuna	Kishinouye (1926); Marr (1948); Eckles (1949); Hotta (1953); Hotta and Ogawa (1955); E. Nakamura (1965); Matsumoto (1961); Waldron and King (1963); Dragovich (1971)
Yellowfin tuna	Kishinouye (1923); Shimada (1951); Reintjes and King (1953); Suda (1953); King and Ikehara (1956); Koga (1958); Matsumoto (1961); Alverson (1963); Mori (1972)
Albacore	Koga (1958); Mori (1972)
Bigeye tuna	Suda (1953); Koga (1958); Mori (1972)
Black marlin, *Makaira indica*	Shimada (1951); Suda (1953); Royce (1957); Yoshida (1971); Mori (1972)
Blue marlin, *Makaira nigricans*	Suda (1953); Royce (1957); Koga (1958); Yoshida (1971); Mori (1972)
White marlin, *Tetrapturus albidus*	Mori (1972)
Striped marlin, *Tetrapturus audax*	Shimada (1951); Royce (1957); Yoshida (1971); Mori (1972)
Longbill spearfish, *Tetrapturus pfluegeri*	Mori (1972)
Shortbill spearfish, *Tetrapturus angustirostris*	Yoshida (1971); Mori (1972)
Sailfish, *Istiophorus platypterus*	Shimada (1951); Yoshida (1971); Mori (1972)
Swordfish, *Xiphias gladius*	Yoshida (1971); Mori (1972)
Chinese mackerel, *Scomberomorus sinensis*	Imamura (1949)
Wahoo, *Acanthocybium solandri*	Iversen and Yoshida (1957)
Escolares, Gempylidae	E. Nakamura (1965)
Thresher shark, *Alopias* sp.	Strasburg (1958)
Requiem shark, *Carcharhinus albimarginatus*	Fourmanoir (1960)
Seabirds	Simmons (1969); Potthoff and Richards (1970)

Fourmanoir, P. 1960. Rapport sur *Katsuwonus pelamis* dans l'ouest de l'ocean Indien. CCTA/CSA (Commission for Technical Cooperation in Africa/Scientific Council for Africa), Colloque sur les Thonidés, Dakar, 12-17 décembre 1960, Tunny (60)9, 9 p.

Table 10.--Parasites of skipjack tuna.

Parasites	Source
Trematodes	
Monogenetic	
Capsala interrupta (Monticelli)	Silas (1967)
Capsala katsuwoni (Ishii)	
Capsala laevis (Verrill)	
Capsala lintoni (Price)	
Capsala nozawae (Goto)	
Hexostoma grossum (Goto)	
Pricea minimae Chauhan	
Pseudaxine katsuwoni Ishii	
Pseudaxine vagans Ishii	
Digenetic	
Atalostrophium (*Atalospargarum*) sp. Ishii	Silas (1967)
Atalostrophion sardae MacCallum	
Didymocylindrus filiformis Ishii	
Didymocystis abdominalis Yamaguti	
Didymocystis bilobata Ishii	
Didymocystis dissimilis Yamaguti	
Didymocystis ovata Ishii	
Didymocystis simplex Ishii	
Didymocystis soleiformis Ishii	
Didymocystis submentalis Yamaguti	
Didymocystis wedli Ariola	
Didymoproblema fusiformes Ishii	
Didymozoon filicolle Ishii	
Didymozoon longicolle Ishii	
Didymozoon minor Yamaguti	Silas (1967)
Dinurus euthynni Yamaguti	
Hirudinella marina (Garsin)	
Koellikeria globosa Ishii	
Koellikeria orientalis (Yamaguti)	
Koellikeria reniformis Ishii	
Lobatozoum multisacculatum Ishii	
Neodiplotrema pelamydes (Yamaguti)	
Syncoelium katuwo Yamaguti	
Cestodes	
Tentacularia coryphaenae (Bosc)	Waldron (1963)
Callotetrarhynchus speciosus (Linton)	
Pelichnibothrium [larva]	
Rhyncobothrium	
Tentacularia bicolor (Bartels)	Silas (1967)
Nematodes	
Anisakis sp. [larva]	Waldron (1963)
Philometroides sp.	
Acanthocephalids	
Nipporhynchus ornatus (Van Cleave)	
Nipporhynchus trachuri (Harada)	Chen and Yang (1973)
Copepods	
?*Anuretes branchialis* Rangneker	Silas and Ummerkutty (1967)
Caligus bonito Wilson	
Caligus mutabilis Wilson	
Caligus pelamydis Kroyer	
Caligus quadratus Shiino	
Caligus coryphaenae Steenstrup and Lütken	Cressey and Cressey (1980)
Caligus productus Dana	
Caligus asymmetricus Kabata	
Pseudocycnus appendiculatus Heller	
Unicolex reductis, new species	
Lepeophtheirus dissimulatus Wilson	Silas and Ummerkutty (1967)
Lepeophtheirus salmonis Kroyer	Waldron (1963)
Homoiotes bermudensis Heegaard	

3.4 Nutrition and growth

3.41 Feeding

(1) Time

Feeding by skipjack tuna follows a more or less regular pattern. From studies of stomach contents, Yuen (1959), Waldron and King (1963), E. Nakamura (1965), and Dragovich (1971) determined that feeding peaks in the early morning from about 0800 to 1200, drops to a low between 1300 and 1600, and peaks again in the late afternoon, roughly from about 1600 to sunset (Fig. 28). E. Nakamura (1965) associated this feeding pattern with the availability of food. He stated, "Zooplankters move downward during the early daylight hours, presumably to reach a preferred level of illumi-

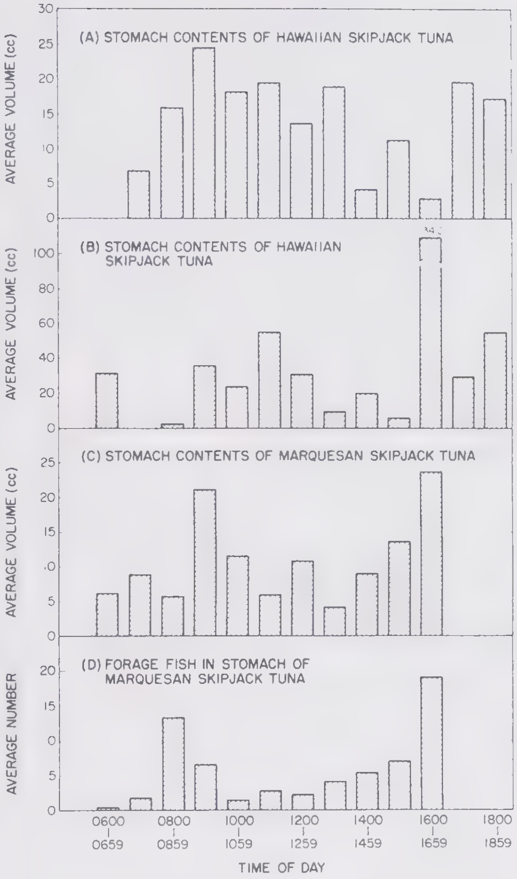

Figure 28.—Diurnal variation in volumes of stomach contents of Hawaiian skipjack tuna (panels A and B) and diurnal variation in volumes (panel C) and number of forage fish (panel d) in stomachs of Marquesan skipjack tuna (data from Waldron and King 1963 (A); Yuen 1959 (B); and E. Nakamura 1965 (C and D)).

nation. Since they serve as food for the forage organisms, some of the latter, also seeking lower levels of illumination, will tend to move downward and thus minimize their availability to the surface-dwelling skipjack. The minima occur around noon, the period when sunlight penetration is greatest, when zooplankters are deepest, and when forage fish are least available to skipjack. During late daylight hours the zooplanters and forage fish begin their upward movement. Skipjack begin feeding heavily in the late afternoon hours before dark as food becomes more available." He suggested also that the diurnal variation in the volumes of stomach contents may also reflect the effects of satiation. He reasoned that "Skipjack, starting the day with their stomachs empty, feed actively during the early morning hours, and food consumption reaches a peak sometime before noon. A period of satiety occurs midday while digestive processes reduce the stomach contents. As the stomach empties, skipjack forage again, and the volume reaches a second peak prior to darkness." That this may not always be the case is suggested in the hourly catches of skipjack tuna in the Hawaiian fishery

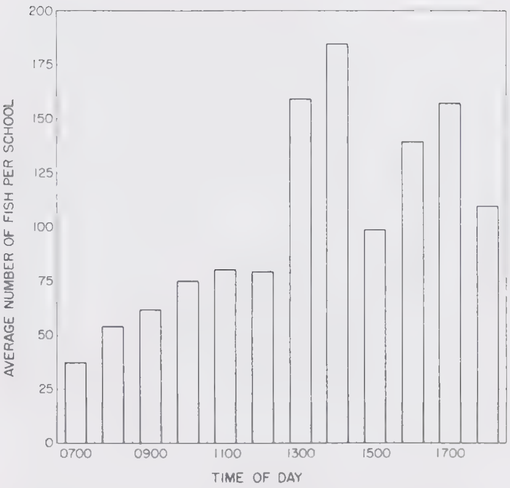

Figure 29.—Skipjack tuna catches by time of day for several Hawaiian bait boats during the 1956 and 1957 fishing seasons (data from Yuen 1959).

(Fig. 29). If the fish were satiated near midday, then chumming with bait, which would involve more feeding, should not result in large catches; yet, the figure shows that the highest average catches occurred at about that time. Hence, E. Nakamura's observation on the association of feeding with the availablility of food is preferable to the latter hypothesis based on volume of stomach content.

Some seasonal variations in feeding are indicated in studies of stomach content volumes but for the most part, the variations reflect the seasonal changes in abundance of forage organisms. Waldron and King (1963) observed a noticeable decrease in the average volumes of food in stomachs collected in Hawaiian waters during midsummer as compared with stomachs collected in late spring and early fall. The trend of the average volume followed closely that of the forage fish component. E. Nakamura (1965) observed that though the occurrence of forage did not vary from season to season in skipjack tuna stomachs from the central equatorial Pacific, the proportions of the three major food categories did so. Crustaceans were low in fall and highest in summer, and molluscs were lowest in spring and highest in fall. In waters around the Laccadive Islands, Raju (1964b) found that the total average forage volume showed a peak in early spring and a lesser peak in the fall. The trend closely followed that of crustaceans, which dominated the food category in the areas sampled.

(2) Food selectivity

It is reasonable to expect that food requirements and the capacity to satisfy the requirements, such as larger mouth and stomach, increase as the size of fish increases. All studies of this relationship (Yuen 1959; Alverson 1963; Waldron and King 1963; Raju 1964b; E. Nakamura 1965) agree that the average volume of food in skipjack tuna stomachs increases with size of fish. Differences in the diet have also been found among the various sizes of skipjack tuna. Generally, the smaller skipjack tuna rely mainly on crustaceans for food;

the larger skipjack tuna, on juvenile and small fishes. Yuen (1959) observed that the percent either by volume or occurrence of fish in stomachs of skipjack tuna collected near Hawaii increased with an increase in size, whereas the percent of molluscs and crustaceans decreased. Similar observations were noted generally for skipjack tuna in the Marquesas Islands (E. Nakamura 1965), eastern Pacific Ocean (Alverson 1963), central Indian Ocean (Raju 1964b), and western Atlantic Ocean, off North Carolina, U.S.A. (Batts 1972b).

Magnuson and Heitz (1971), in their study of the gill raker apparatus among scombrids and dolphins (Coryphaenidae), found that gill raker gap differed markedly among species and lengths of fish. A 50 cm skipjack tuna, a 30 cm yellowfin tuna, and a 10 cm striped bonito, *Sarda orientalis*, all had an estimated gill raker gap of 1 mm; and conversely, the gaps of a 50 cm fish of each species were estimated to be ca. 1.0, 1.7, and 4.5 mm, respectively (Fig. 30). Comparing mean gill raker gap with the stomach contents of fishes based on the literature, they showed that the percent volumes of crustaceans were inversely related to mean gill raker gaps and concluded that gill raker gap was related functionally with the quantity of smaller organisms in the stomachs. The presence of euphausids in stomachs of skipjack tuna and their absence in yellowfin tuna were cited as evidence for selection of organisms as determined by the magnitude of the gill raker gaps.

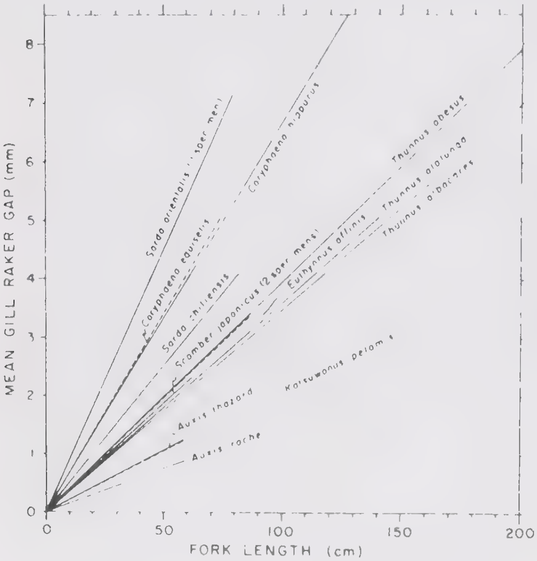

Figure 30.—Comparison of the mean gill raker gap and fork length relationship for various scombrid and coryphaenid fishes. Lengths are approximate ranges known for each species (from Magnuson and Heitz 1971).

(3) Distance from land

In examining feeding with respect to distance from land, arbitrarily zoned at 16, 40, 80, 161, and 322 km (10, 25, 50, 100, 200, and over 200 mi), Waldron and King (1963) found the average volume of stomach contents increased with distance from shore up to 50 mi and varied irregularly at greater distances. The trend was due largely to variation in the volume of fishes, which were the dominant food element. Among the families of fish consumed, Scombridae, Mullidae, and Carangidae were important within 16 km; Scombridae was dominant between 40 and 80 km, followed by Carangidae, Gempylidae, and Holocentridae; and Scombridae, Gempylidae, and Exocoetidae were important in offshore areas between 161 and 322 km. E. Nakamura (1965) found no relationship between stomach content volumes and distance from land of skipjack tuna taken around the Marquesas Islands. He noted, however, that food items categorized as reef-originating forms decreased significantly from inshore to offshore along four 362 km (225 mi) survey tracks. The percentages of reef-originating forms in the inner, middle, and outer 121 km (57 mi) sectors were 61.5, 39.9, and 8.8, respectively.

(4) Feeding behavior

Only a few studies have been made of the feeding behavior of skipjack tuna both in the wild and in captivity, but these have provided a wealth of information. Nakamura (1962), from his study of skipjack tuna in captivity, found that 1) when fed hourly until satiated, skipjack tuna exhibited an initial high feeding followed by feeding of small amounts throughout the day; 2) skipjack tuna had difficulty in seizing the food at night; 3) new fish introduced into tanks learned to feed faster when experienced fish were already in the tanks; 4) food particles were always taken at the surface or middepth, never off the bottom, and swimming was often accelerated prior to taking the food; 5) they rejected whole shrimp or squid after ingesting a few pieces, but when the rejected pieces were cut up into smaller pieces, the food was again accepted; and 6) captive skipjack tuna were never seen to prey upon small fish which were present in the pool.

Magnuson (1969) studied other aspects of feeding behavior of skipjack tuna in captivity. In one experiment, skipjack tuna were fed at intervals of 15 min throughout the day. A period of intense feeding occurred between 0630 and 0830 (Fig. 31). During this period the fish did not fill their stomachs to capacity the first or even the second or third time they were offered food, but filled their stomachs slowly over the whole 2-h period. The maximum capacity of the stomach was about 7% of the body weight, but during the whole day the fish ate an equivalent of 15% of their body weight, and the stomachs were completely empty by dawn. In another experiment, skipjack tuna that had been deprived of food for 24 h were fed at a uniform rate for 45 min from 0900 to 0945. The stomach contents approached a maximum after about 30 min (Fig. 32-I). The proportion of food particles attacked decreased as the stomachs filled (Fig. 32-II), but very little change was noted until the contents exceeded 50% of the stomach's capacity. Then the likelihood that a skipjack tuna would attack a food particle decreased rapidly, indicating that satiation had occurred. The fish responded to food particles (i.e., food particles responded to but not attacked) even when the stomach was full (Fig. 32-III).

Passage of food through the alimentary canal was estimated from 54 fish, 39 to 50 cm FL, that had been denied food during the previous 24 h. These fish were fed as many thawed smelt as they would eat and their stomachs and intestines were examined at intervals over a 24-h period. The skipjack tuna ate the equivalent of about 8.6% of their body

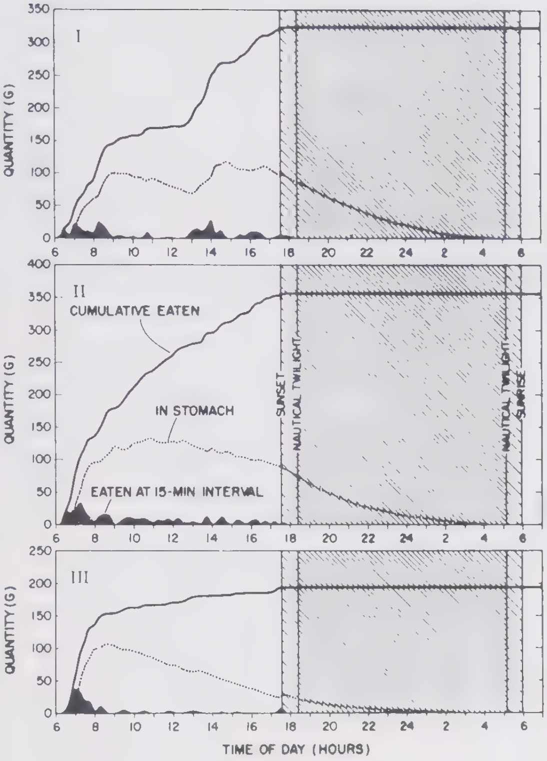

Figure 31.—Diel changes in the feeding of skipjack tuna in captivity. I. Quantity of food eaten. II. Cumulative weight of food eaten. III. Estimated weight of material in the stomach prior to each meal. Food was offered at 15-min intervals from 0600 to 1845 (from Magnuson 1969).

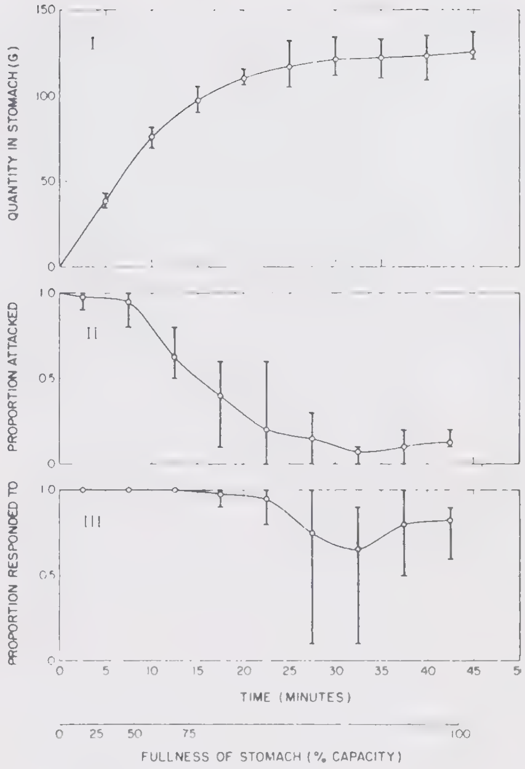

Figure 32.—Changes in feeding behavior as skipjack tuna eats a meal. I. Estimated weight of material in stomach. II. Proportion of food particles attacked. III. Proportion of particles eliciting a response. Means and ranges shown in each plot. Proportion of stomach filled, shown along the time axis, was estimated from panel I (from Magnuson 1969).

weight; about 10% of the initial quantity eaten had passed from the stomach each hour during the first 8 h; and the stomachs were essentially empty within 12 h after a meal. Magnuson (1969) noted also that the contents of the intestine increased rapidly during the first 3 h after the meal and the intestine was essentially empty about 14 h after the meal. Most waste material was evacuated from the intestine while the intestine was being filled from the emptying stomach. Defecation soon after eating was not surprising because of the short intestine in skipjack tuna.

Another aspect of feeding behavior is the appearance of banded color patterns on the skipjack tuna. Strasburg and Marr (1961) reported the appearance of such coloration on skipjack tuna weighing from 1 to over 14 kg, but the bands or bars were not observed on all members of a school. As they explain it, the bands are formed when the dark horizontal stripes are interrupted by light vertical bars. The transitory barred or banded appearance is likely under various conditions and is produced presumably by the contraction of melanophores. The vertical bars were noticed from a ship's subsurface viewing chamber during the chumming of fish schools. Nakamura (1962) confirmed the relation of the appearance of the bars to feeding among skipjack tuna held in captivity. In his feeding experiments he noted that, in addition to excited swimming behavior during feeding, the skipjack tuna exhibited such bars or bands, which disappeared when the fish were no longer interested in food.

Similar markings have been reported for Pacific bonito, *Sarda chiliensis* (Magnuson and Prescott 1966), kawakawa (Nakamura and Magnuson 1965), and dolphin (Strasburg and Marr 1961).

3.42 Food

Various authors have examined the food of skipjack tuna (Kishinouye 1923; Suyehiro 1938; Welsh 1949; Ronquillo 1954; Hotta and Ogawa 1955; Postel 1955; Tester and Nakamura 1957; Yuen 1959; Alverson 1963; Waldron and King 1963; Raju 1964b; Thomas 1964; E. Nakamura 1965; Sund and Richards 1967; Dragovich 1971; Batts 1972b; Roberts 1972). In addition, there are other reports with brief mention of the food of skipjack tuna. The most comprehensive studies to date are those by Hotta and Ogawa (1955), Alverson (1963), Waldron and King (1963), and E. Nakamura (1965) in the Pacific Ocean; Dragovich (1971) and Batts (1972b) in the Atlantic Ocean; and Raju (1964b) in the Indian Ocean.

The major food items fall into three groups: fishes, crustaceans, and molluscs. Although fishes comprise the most important source of food for skipjack tuna in most of the oceans, variations in the order of importance of the major groups of food organisms are found in different areas and seasons (Table 11). In the western and central Pacific and western Atlantic Oceans, fishes (49-95% of total volume) comprised the most important group, followed by molluscs (4-50%), and crustaceans (1-23%) (Welsh 1949; Ronquillo 1954; Waldron and King 1963; Dragovich 1971; Batts 1972b). Waldron and King (1963) reported differences in the food composition of skipjack tuna by island areas in the central Pacific: "(1) Skipjack from the Hawaiian area depended on fishes to a greater extent than those from the Phoenix or Line Islands; (2) skipjack from the Phoenix Island area utilized molluscs, crustaceans, and fishes equally as sources of food; and (3) skipjack from the Line Islands area depended on fishes to a lesser degree than those from the other two areas and to a greater extent on squids and crustaceans." In the eastern sides of the Pacific and Atlantic Oceans, crustaceans were the main source of food. They comprised 50-62% of the food, fish comprised 33-37%, and molluscs, 4-13% (Schaefer 1960; Alverson 1963; Dragovich 1971). In the Indian Ocean around the Laccadive Islands, crustaceans were the most important food group. They made up 59% of the total volume, molluscs were 22%, and fish were 10% (Raju 1964b). At nearby Minicoy Island fishes formed 48% of the food, crustaceans 47%, and miscellaneous items, mostly molluscs, 5% (Thomas 1964).

The food of skipjack tuna in all the major oceans includes a wide variety of organisms, representing 11 invertebrate orders and 80 or more fish families (Table 12). Past studies show that of the invertebrates, two groups of arthropods (decapods and stomatopods) and two groups of cephalopods (octopods and squids) were found in stomachs from nearly all localities. The fish families represented in stomach contents vary considerably, with samples taken in the Pacific Ocean having the greatest number by far. Hotta and Ogawa (1955) listed 48 families, Waldron and King (1963) listed 42, and both Ronquillo (1954) and E. Nakamura (1965) listed 33. In the Atlantic Ocean, Dragovich (1970) listed 28 fish families in the western and 21 in the eastern sectors. Raju (1964b) listed only 10 fish families in the stomachs of skipjack tuna collected from inshore waters (about 8 km) around Laccadive Islands and Thomas (1964) listed 11 fish families from Minicoy Island in the Indian Ocean. Of the fish families represented in the diet of the skipjack tuna, only two, Carangidae and Balistidae, were common to all areas of all oceans. Others that were common to most of the areas were Exocoetidae, Syngnathidae, Holocentridae, Bramidae, Chaetodontidae, Gempylidae, Scombridae (including the tunas), Ostraciidae, and Tetraodontidae.

The presence of scombrids in the stomachs of skipjack tuna deserves special consideration, since this group of fish occasionally constitute a major portion of the skipjack tuna diet. Data from Waldron and King (1963) indicate that scombrids occurred in 10.6% of 707 skipjack tuna stomachs examined and that this group comprised 25.0% of the total volume, the highest of all fish families and larger than the entire mollusc group. E. Nakamura (1965) reported the occurrence of juvenile tuna in 24.8 to 44.2% of 603 stomachs examined from five cruises around the Marquesas and Tuamotu Islands. This group ranked the highest among all fish families on four cruises and fifth on one cruise. Dragovich (1971) also indicated high (25.0%) occurrence of scombrids in 369 skipjack tuna stomachs from the Caribbean Sea and adjacent waters. This group ranked second only to the large unidentified fish group.

The wide variety of food organisms in the stomach contents and the variations in the importance of the major food groups have led to the conclusion that skipjack tuna are opportunistic feeders and will prey upon any forage organisms that are available to them. Cannibalism among the skipjack tuna lends additional support to this conclusion. In the central Pacific Ocean, E. Nakamura (1965) reported juvenile skipjack tuna in 12.4% of the skipjack tuna stomachs containing food. He also indicated that 7.8% of 707 stomachs collected by Waldron and King (1963) contained juvenile skipjack tuna. Conand and Argue (1980) reported that 3.3% of 5,956 stomachs of skipjack tuna from the western Pacific Ocean (lat. 25°N-42°S, long. 134°E-140°W) contained juvenile skipjack tuna. In the Atlantic Ocean, Suarez Caabro and Duarte-Bello (1961) and Dragovich (1971) also reported the occurrence of juvenile skipjack in stomachs of skipjack tuna.

3.43 Growth rate

Various methods have been used to determine the growth of skipjack tuna and other tunas, including analyses of growth

Table 11.—Percent composition of the three major food groups of skipjack tuna in various localities.

Author	Locality	Percent of total volume		
		Fishes	Crustaceans	Mollusks
Ronquillo (1954)[1]	Western Pacific-Sulu, Celebes Sea	66	23	11
Waldron and King (1963)	Central Pacific-Hawaii, Line, Phoenix Is.	75	4	20
Welsh (1949)	Central Pacific-Hawaii (live-bait fishery)	63	9	28
Welsh (1949)	Central Pacific-Hawaii (trolling)	51	27	22
Schaefer (1960)	Eastern Pacific	33	62	4
Alverson (1963)	Eastern Pacific	37	59	3
Batts (1972b)	Western Atlantic-Cape Hatteras	90	3	7
Batts (1972b)	Oregon Inlet, western Atlantic-North Carolina, U.S.A.	49	1	50
Dragovich (1971)	Western Atlantic, Equatorial	95	1	4
Dragovich (1971)	Eastern Atlantic, Equatorial	37	50	13
Raju (1964a)	Central Indian-Laccadive Islands	19	59	22
Thomas (1964)	Central Indian-Minicoy Islands	48	47	5

[1] The percentages are of number of organisms. Conversion to percentages of volume would rank the mollusks second and the crustaceans third.

Table 12.—Organisms found in skipjack tuna stomachs by various authors.

	Pacific Ocean							Atlantic Ocean			Indian Ocean
	Hotta and Ōgawa (1955) Japanese waters	Ronquillo (1954) Philippine waters	Welsh (1949) Hawaiian waters	Yuen (1959) Hawaiian waters	Waldron and King (1963) Hawaii, Line, and Phoenix	Nakamura, E. (1965) Marquesas and Society Is.	Alverson (1963) Eastern Pacific	Dragovich (1971) Western Atlantic	Batts (1972b) Western Atlantic	Dragovich (1971) Eastern Atlantic	Raju (1964b) Central Indian
	Number of samples										
Taxonomic group	2,900	115	224	573	707	603	2,317	1,060	705	1,060	2,609
Arthropoda	x	x	x	x	x	x	x	x	x	x	x
Crustacea	x	x	x	x	x	x	x	x	x	x	x
Copepoda					x						
Mysidacea					x		x			x	x
Isopoda				x	x		x	x	x		
Amphipoda		x		x	x	x	x	x	x	x	
Euphausiacea	x			x	x	x	x			x	x
Decapoda	x	x	x	x	x	x	x	x	x	x	
Stomatopoda		x	x	x	x	x	x	x	x	x	x
Mollusca	x	x	x	x	x	x	x	x	x	x	x
Gastropoda					x	x	x	x	x	x	
Heteropoda					x	x		x	x	x	
Pteropoda					x	x	x	x	x	x	
Cephalopoda	x	x	x	x	x	x	x	x	x	x	x
Octopoda	x	x	x	x	x	x	x	x	x	x	x
Decapoda	x	x	x	x	x	x	x	x	x	x	x
Chordata	x	x	x	x	x	x	x	x	x	x	x
Tunicata					x	x	x			x	x
Pisces	x	x	x	x	x	x	x	x	x	x	x
Albulidae					x						
Clupeidae	x	x			x				x		
Dussumieriidae (= Clupeidae)	x		x								
Engraulidae							x				
Gonostomatidae	x						x				
Sternoptychidae	x	x			x		x				
Stomiatidae		x			x						
Idiacanthidae						x					
Synodontidae		x	x	x	x	x				x	
Paralepidae (= Sudidae)	x	x		x	x		x	x		x	
Alepisauridae	x	x			x						
Myctophidae (= Scopelidae)	x	x			x	x	x			x	
Congridae									x	x	
Belonidae					x	x					
Scomberesocidae	x				x		x				
Hemiramphidae		x			x		x				
Exocoetidae	x	x				x	x	x	x		
Oxyporhamphidae (= Hemiramphidae)	x	x				x	x	x	x		
Gadidae							x		x		
Aulostomidae			x								
Fistulariidae		x		x	x	x	x				
Macrorhamphosidae	x										
Syngnathidae		x	x	x	x			x	x	x	
Holocentridae	x	x	x	x	x	x		x	x		
Grammicolepidae	x										
Antigoniidae (= Caproidae)		x		x				x			
Sphyraenidae	x			x	x	x					
Atherinidae					x						
Polynemidae	x						x	x			
Serranidae	x			x		x	x	x		x	
Epinephelidae (= Serranidae)	x										
Kuhliidae					x						
Priacanthidae	x	x	x	x	x	x		x		x	
Malacanthidae								x			
Scombropidae					x						
Labracoglossidae	x										
Carangidae	x	x	x	x	x	x	x	x	x	x	x
Menidae	x										

Table 12.—*Continued.*

	Pacific Ocean							Atlantic Ocean			Indian Ocean
	Hotta and Ogawa (1955) Japanese waters	Ronquillo (1954) Philippine waters	Welsh (1949) Hawaiian waters	Yuen (1959) Hawaiian waters	Waldron and King (1963) Hawaii, Line, and Phoenix	Nakamura, E. (1965) Marquesas and Society Is.	Alverson (1963) Eastern Pacific	Dragovich (1971) Western Atlantic	Batts (1972b) Western Atlantic	Dragovich (1971) Eastern Atlantic	Raju (1964b) Central Indian
	Number of samples										
Taxonomic group	2,900	115	224	573	707	603	2,317	1,060	705	1,060	2,609
Bramidae		x	x	x	x	x		x	x	x	
Coryphaenidae	x	x			x	x		x	x		
Emmelichthyidae	x					x					
Lutianidae	x					x					
Caesionidae (= Lutianidae)	x	x									
Sciaenidae							x				
Denticidae (= Lethrinidae)	x										
Mullidae	x	x	x	x	x	x		x			
Pampheridae	x										
Kyphosidae						x					
Ephippidae									x		
Chaetodontidae	x	x	x	x	x	x	x	x		x	
Pomacanthidae (= Chaetodontidae)					x						
Pomacentridae		x		x		x					
Cirrhitidae				x							
Chiasmodontidae		x						x		x	
Blenniidae				x	x	x					
Brotulidae					x						
Ophidiidae									x		
Ammodytidae	x			x	x	x					
Callionymidae							x				
Siganidae	x	x									
Zanclidae	x										
Acanthuridae	x		x	x	x	x		x	x		
Teuthidae (= Acanthuridae)		x								x	
Gempylidae	x	x	x	x	x	x		x	x	x	
Trichiuridae	x	x					x			x	
Scombridae (+ Thunnidae)	x	x	x	x	x	x	x	x	x	x	
Scomberomoridae (= Cybiidae)	x				x						
Istiophoridae	x								x		
Tetragonuridae					x						
Stromateidae								x	x		
Nomeidae	x			x	x	x					
Centrolophidae (= Nomeidae)			x								
Scorpaenidae				x	x	x		x		x	
Triglidae			x								
Peristediidae (= Triglidae)	x										
Platycephalidae						x					
Dactylopteridae		x		x		x		x	x	x	x
Bothidae										x	
Echeneidae	x										
Triacanthidae		x									x
Balistidae	x	x	x	x	x	x	x	x		x	x
Monacanthidae (= Balistidae)	x		x		x	x		x	x	x	x
Ostraciidae	x	x	x	x	x	x	x	x			x
Tetraodontidae	x	x		x	x			x	x	x	x
Canthigasteridae (= Tetraodontidae)	x				x						
Diodontidae	x	x		x	x	x		x			
Molidae	x			x	x			x			
Lophiidae							x				
Antennariidae											x
Pegasidae				x		x					

marks on hard parts such as vertebrae (Aikawa 1937; Aikawa and Kato 1938; Yokota et al. 1961; Chi and Yang 1973), first dorsal spine (Shabotiniets 1968; Batts 1972a), and otoliths (Wild and Foreman 1980; Uchiyama and Struhsaker 1981); temporal progression of length-frequency modes (Brock 1954; Kawasaki 1955a, b, 1963, 1965a; Schaefer 1961a; Yokota et al. 1961; Joseph and Calkins 1969; Yoshida 1971; Chi and Yang 1973); and data from tagged fish (Schaefer et al. 1961; Rothschild 1967; Joseph and Calkins 1969; Josse et al. 1979). Reviews of some of these studies were given by Shomura (1966a), Rothschild (1967), Joseph and Calkins (1969), Chi and Yang (1973), and Josse et al. (1979). A summary of the results of these studies is presented in Table 8 and representative growth curves are shown in Figures 33-35.

Josse et al. (1979) reviewed the methods and results of most of the studies made to date and have concluded that counting seasonal growth marks on vertebrae, scales, and dorsal spines and following modal progressions of length frequencies were least reliable, that counting daily increments on otoliths was more reliable, and that measuring growth between tagging and recapture was the most reliable. Their low regard for counting growth marks and for following modal progressions stemmed from the failure of investigators to show irrefutably the periodicities in the appearance of growth rings and from the results of their own analysis of length-frequency data. They found that clear progressions of modes for more than a few months, other than in exceptional instances, were difficult to demonstrate and that the apparent modal progression could give in a single region, in different years, growths which were rapid, slow, nil, and even negative. They pointed out, first, the inadequacy of determining growth from otolith increments to resolve the problem of age, should the skipjack tuna pass through phases of no growth during the breeding period, and second, the uncertainty in reading daily marks close to the nucleus (Lewis[8]).

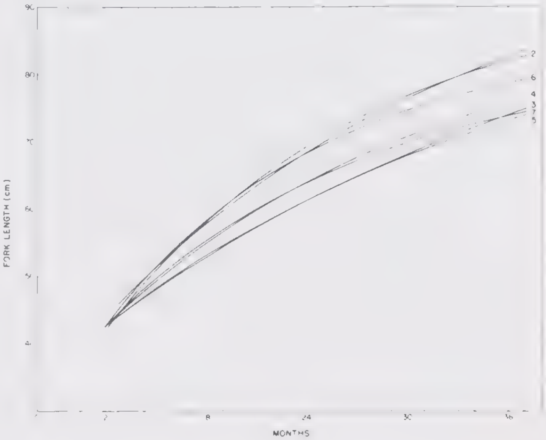

Figure 34.—Growth estimates of central Pacific skipjack tuna. 1) Uchiyama and Struhsaker (1981), otolith increments; 2) Skillman, tag returns, males only (see text footnote 10); 3) Rothschild (1967), tag returns, uncorrected data; 4) Skillman, tag returns, males and females (see text footnote 10); 5) Brock (1954), modal progression; and 6) Rothschild (1967), tag returns, corrected data (from Uchiyama and Struhsaker 1981).

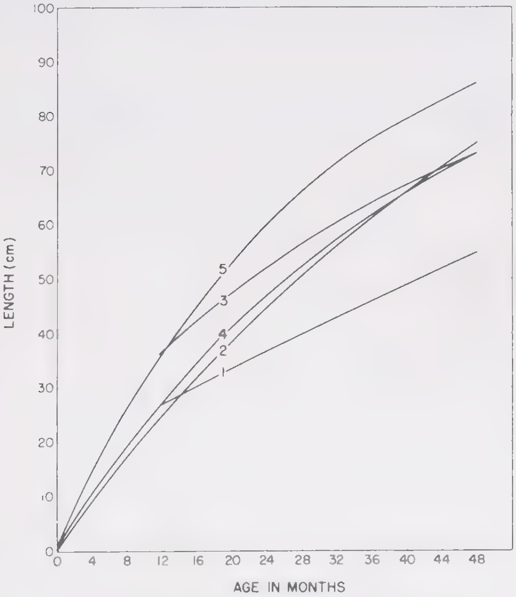

Figure 33.—Growth estimates of western Pacific skipjack tuna. 1) Aikawa and Kato (1938), vertebral rings; 2) Kawasaki (1963), modal progression (Joseph and Calkins 1969; 3) Yokota et al. (1961), modal progression; 4) Chi and Yang (1973), vertebrae; and 5) Chi and Yang (1973), modal progression.

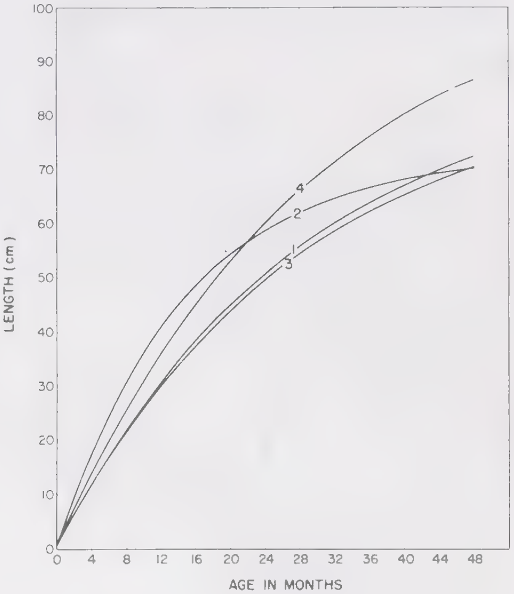

Figure 35.—Growth estimates of eastern Pacific skipjack tuna. 1) Joseph and Calkins (1969), tag returns, averaged data; 2) Joseph and Calkins (1969), tag returns, nonaveraged data; 3) Schaefer (1961a), modal progression; and 4) Joseph and Calkins (1969), modal progression (from Joseph and Calkins 1969).

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[8] Lewis, A. D. 1976. The relevance of data collected in Papua New Guinea to skipjack population studies in the western Pacific. Document 1066/76, 5 p. Department of Primary Industry, Papua New Guinea. Ministry of Agriculture, Forests, and Fisheries, Fisheries Division, Suva Fiji.

While Josse et al. (1979) considered tagging data to be the most reliable, the possibility of an interruption in growth caused by tagging itself has yet to be determined. We cite as an example the work by Wild and Foreman (1980), who investigated the relation of otolith increments and time for tagged and recaptured skipjack and yellowfin tunas marked with tetracycline. They observed that the number of increments underestimated time by approximately 24% during growth from 42 to 64 cm over a period of up to 249 d. They further reported that the growth rate of skipjack tuna, estimated from the length at recapture and linear change in otolith dimension of tagged fish injected with tetracycline was 1.15 cm/mo. The growth rate was comparable with that obtained from earlier tagging studies by Joseph and Calkins (1969) in the eastern Pacific, but much less than that estimated from the latter's results based on modal progression. The agreement of the growth rates from otolith increments after tetracycline treatment and from incremental change in size indicates that both methods are equally good at measuring growth rate of tagged fish but provide no information on the effect of tagging itself.

The matter of reliability in the length of fish at release should be considered also in tagging data. In most past studies the average length of fish from the same school was assigned to the tagged fish or tagged fish were measured to the nearest 5 cm. Only recently in Papua New Guinea (Josse et al. 1979) and in the eastern Pacific (IATTC[9]) have tagged fish been measured more closely at time of release, i.e., to the nearest centimeter. Until similar data are obtained from other areas and the adverse effects of handling fish during tagging have been clarified, the age and growth of skipjack tuna must be considered only as approximations.

Growth estimates of skipjack tuna in the western North Pacific have been determined only from analysis of vertebrae and modal progression. Aikawa (1937) and Aikawa and Kato (1938) made no serious attempt to validate growth rings as annual marks. Their lengths at age appear to be greatly underestimated. Chi and Yang (1973), using both methods, observed that two rings were formed annually on vertebrae of skipjack tuna taken from waters around Taiwan and that growth estimates from modal progression were higher than those obtained from growth marks on vertebrae (Table 8; Fig. 33). The growth of skipjack tuna, based on modal progression, was 24 cm from age 12 to 24 mo and 15 cm from age 24 to 36 mo. Growth estimates from modal analysis by Yokota et al. (1961) were lower than those obtained by Chi and Yang (1973) and comparable with the latter's estimates from vertebral analysis.

Growth estimates of skipjack tuna in the central and eastern Pacific have been obtained from modal progression, otolith increments, and tagging (Figs. 34, 35). Growth estimated from modal progresssion in both areas was comparable with that obtained by Chi and Yang (1973) in the western North Pacific and generally higher than that estimated from tagging. Growth between ages 12-24 and 24-36 mo were 25 and 11 cm, respectively, in the central Pacific (Uchiyama and Struhsaker 1981) and 23 and 16 cm, respectively, in the eastern Pacific (Joseph and Calkins 1969).

Uchiyama and Struhsaker (1981) obtained growth estimates from otolith increments of skipjack tuna in Hawaiian waters. Their estimates varied somewhat from those obtained from modal progressions in the same area and in the eastern and western Pacific (Joseph and Calkins 1969; Chi and Yang 1973). Although growth was similar for fish increasing in age from 12 to 24 mo (24 cm), it was much higher for fish increasing in age from 24 to 36 mo (25 cm).

Growth estimates derived from tagging show little or no difference for fish in the central and eastern Pacific (Table 8). Growth of fish increasing in age from 12 to 24 mo and 24 to 36 mo were 18-23 and 9-13 cm, respectively, in Hawaiian waters (Joseph and Calkins 1969, Skillman[10]) and 18-20 and 8-13 cm, respectively, in the eastern Pacific (Joseph and Calkins 1969).

Tagging studies in Papua New Guinea by Kearney (1978) have indicated that skipjack tuna in that region grew at an average annual rate of 7 cm. The estimate was derived from fish between 2 and 6 kg (ca. 38.0-64.4 cm) which were at liberty for up to 789 d. Kearney stated "The available tagging information . . . leaves little doubt that the growth rate and maximum size of skipjack in the western subpopulation are much lower than that for the more easterly subpopulations." Subsequent aging studies from otoliths (Uchiyama and Struhsaker 1981; Fig. 36) and tagging by Josse et al. (1979) and the IATTC (footnote 9) have confirmed this. Josse et al. (1979) analyzed published and unpublished tagging data from the eastern Pacific, Hawaii, and Papua New Guinea and determined that the lowest growth rates were observed in skipjack tuna from Papua New Guinea and the highest from Hawaii. The IATTC (footnote 9) compared new tagging data (fish length at release measured to nearest centimeter) from the eastern Pacific with similar data from Papua New Guinea

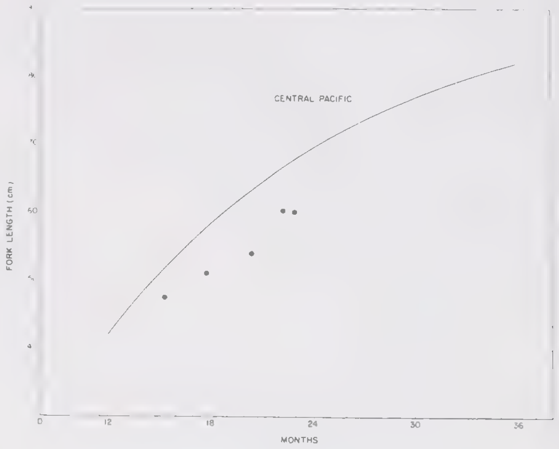

Figure 36.—Age of skipjack tuna from Papua New Guinea (dots) compared with the von Bertalanffy growth curve of central Pacific skipjack tuna (from Uchiyama and Struhsaker 1981).

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[9] Inter-American Tropical Tuna Commission. 1981. The bi-monthly report. January-February 1981. Inter-Am. Trop. Tuna Comm., 21 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

[10] Skillman, R. A. Estimates of von Bertalanffy growth parameters for skipjack tuna, *Katsuwonus pelamis*, from capture-recapture experiments in the Hawaiian Islands. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

and found that skipjack tuna in the eastern Pacific grew at a significantly faster rate than those in the Papua New Guinea region.

Studies of skipjack tuna age and growth in the Indian and Atlantic Oceans have been minimal. Shabotiniets (1968) determined the size at age of skipjack tuna in the Indian Ocean from growth marks in the first spine of the first dorsal fin (Table 8). Since he did not validate these marks as annuli, the size at age he obtained thus appears questionable. Batts (1972a) also made a study of the growth and age of skipjack tuna from growth marks in the first dorsal spine of fish from the western Atlantic Ocean. He, too, failed to show that the growth marks were annuli. His sizes at ages 1 through 4 essentially represent a straight line and differ greatly from that obtained by others using data on modal progression or tag returns (Table 8).

3.5 Behavior

See Section 3.41(4) for feeding behavior; Section 3.13 for reproductive behavior.

3.51 Migrations and local movements

Migrations of skipjack tuna have been determined for certain areas and hypothesized for others through various methods, such as following the movement through a fishery of fish groups identified by size or age, from tagging, population genetic studies, and from tuna longline catch data. The most direct evidence has been from tagging data, but there is one weakness in this method—it only gives the net movement from point of release to point of recapture and does not show the actual path taken by the fish in the interim.

In the central-eastern Pacific, Rothschild (1965), on the basis of available evidence on larval distribution, gonad indices, size distributions, tag recoveries, catch predictions, and immunogenetic studies, hypothesized that a large portion of the skipjack tuna taken in the eastern Pacific Ocean originate in the equatorial Pacific; that a large component of prerecruits (<35 cm) moves eastward and is split into a northern group that enters the Baja California fishery area and a southern group that enters the Central and South American fishery areas; and that the skipjack tuna remain in the eastern Pacific for several months before they move offshore into equatorial waters to spawn (Fig. 37).

A tagging study by Fink and Bayliff (1970) showed detailed movements of skipjack tuna in the eastern Pacific fisheries (Fig. 38). They reported that there appear to be two main

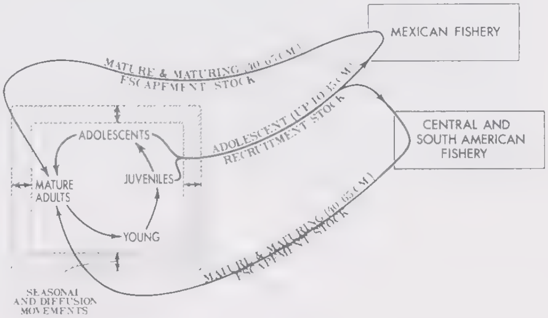
MEXICAN FISHERY
MATURE & MATURING (40-65 CM) ESCAPEMENT STOCK
ADOLESCENT (UP TO 35 CM) RECRUITMENT STOCK
CENTRAL AND SOUTH AMERICAN FISHERY
ADOLESCENTS
MATURE ADULTS
JUVENILES
YOUNG
MATURE & MATURING (40-65 CM) ESCAPEMENT STOCK
SEASONAL AND DIFFUSION MOVEMENTS

Figure 37.—Hypothesized origin and migration of skipjack tuna between the central equatorial Pacific and the northern (Mexican) and southern (Central and South America) fisheries of the eastern Pacific Ocean (from Rothschild 1965).

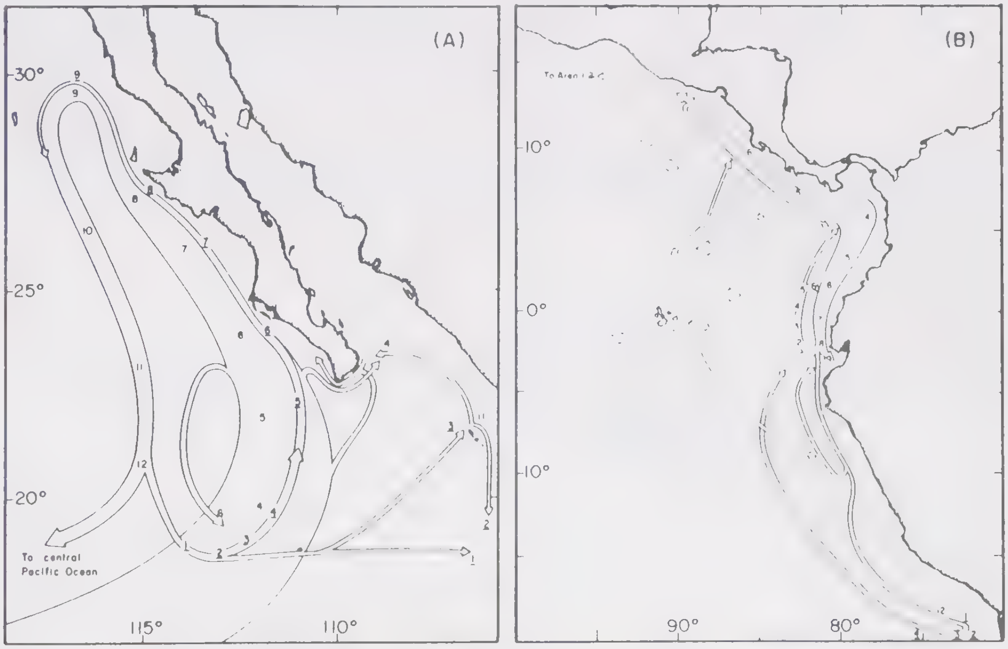
(A)
30°
25°
20°
To central Pacific Ocean
115°
110°
(B)
To Area 1 & 2
10°
0°
10°
90°
80°

Figure 38.—Inshore migration of skipjack tuna of the A) northern fishery group and B) southern fishery group based on tagging data; numbers refer to months (from Fink and Bayliff 1970).

groups of skipjack tuna in the eastern Pacific; that recruits to the northern fishery first enter the fishery in the Revillagigedo Islands in April, migrate north along the Baja California coast during spring and summer, return south in the fall, and then migrate to the central Pacific; and that recruits to the southern fishery enter the fishing area in or near the Panama Bight and migrate both northwest to Central America and south to the Gulf of Guayaquil. Although a few fish tagged off Ecuador in the Gulf of Guayaquil were recovered off Baja California, they reported little interchange of skipjack tuna between the northern and southern fisheries.

Williams (1972) has extended Rothschild's hypotheses by proposing three migration models for the recruitment of skipjack tuna into the eastern Pacific fisheries: An active migration model (Fig. 39A), where the fish migrate eastward actively along zonal productivity bands at the northern and southern edges of the North Equatorial Countercurrent (NECC); a passive migration model (Fig. 39B), where the fish are passively carried eastward in the equatorial countercurrents; and a gyral migration model (Fig. 39C), which involves both active and passive migration. In the last model Williams proposed that the fish of the northern group move counterclockwise around a zonally narrow equatorial gyre consisting of the NECC and the North Equatorial Current, with the western limit some distance west of long. 130°W; and that fish of the southern group move eastward in the NECC and return to the central Pacific in the South Equatorial Current.

Recoveries in Hawaii of skipjack tuna tagged in the eastern Pacific showed the capability of the skipjack tuna to negotiate long migrations. Seckel (1972) developed a numerical drift simulation model based on geostrophic and wind-driven currents as a potential mode of skipjack tuna migration from the eastern Pacific northern fishery into Hawaiian waters. He determined that fish could drift from an area between lat. 10° and 20°N at long. 120°W to an area between lat. 19° and 22°N at long. 155°W in 21 to 23 mo (Fig. 40). Although the time intervals are within the range of values for skipjack tuna tagged in the eastern Pacific and recaptured in Hawaii, they are, by far, longer than most (Table 13).

In the northwestern Pacific for fish caught in the Japanese coastal fisheries, Imamura (1949) noted that skipjack tuna migrated annually from the southern seas northward in the warm Kuroshio in the spring and summer and returned south as the cold Oyashio became stronger in the fall. Kawasaki (1955a, b) proposed that there are two groups of skipjack tuna in the southwestern Japanese waters which migrate north from the Ryukyu Islands to southern Japan and back,

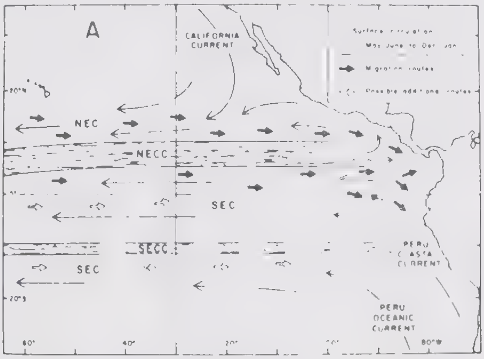
A
CALIFORNIA CURRENT
Surface circulation May/June to Dec./Jan.
Migration routes
Possible additional routes
20°N
NEC
NECC
SEC
SECC
SEC
PERU COASTAL CURRENT
20°S
PERU OCEANIC CURRENT
160°
140°
120°
100°
80°W
B
CALIFORNIA CURRENT
Surface circulation Jan./Feb. to April/May
Migration routes
Possible additional routes
20°N
NEC
NECC
SEC
SECC
SEC
PERU COASTAL CURRENT
20°S
PERU OCEANIC CURRENT
120°
100°
80°W

Figure 39A.—Active migration model: A) routes of young skipjack tuna into the southern fishery and B) routes of young skipjack tuna into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent. (From Williams 1972.)

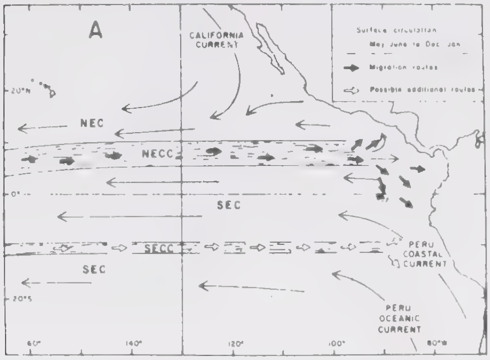
A
CALIFORNIA CURRENT
Surface circulation May/June to Dec./Jan.
Migration routes
Possible additional routes
20°N
NEC
NECC
0°
SEC
SECC
SEC
PERU COASTAL CURRENT
20°S
PERU OCEANIC CURRENT
160°
140°
120°
100°
80°W
B
CALIFORNIA CURRENT
Migration routes
Possible additional routes
20°N
NEC
NECC
0°
SEC
SECC
SEC
PERU COASTAL CURRENT
20°S
PERU OCEANIC CURRENT
160°
140°
120°
100°
80°W

Figure 39B.—Passive migration model: A) routes of young skipjack tuna into the southern fishery and B) routes of young skipjack tuna into the northern fishery. See Figure 39A for abbreviations. (From Williams 1972.)

and two groups (coastal and offshore) in the southeastern and eastern Japanese waters which migrate north and south at different times of the year. Based on the similarity of fish sizes taken in the Japanese, Hawaiian, and eastern Pacific fisheries, he proposed (1964, 1965b) that the skipjack tuna in the northwestern Pacific is closely related to skipjack tuna taken in Hawaii and the eastern Pacific; that the major spawning area is centered along the Equator west of long. 140°W; that the larvae spawned there in summer migrate to the fisheries area by winter and are recruited into the fisheries at age 2; and that these fish migrate southward at age 3 and remain in the equatorial spawning area from ages 3.5 to 5.5.

Fujino (1972), on the basis of population genetic studies (see Section 1.33), recognized two subpopulations of skipjack

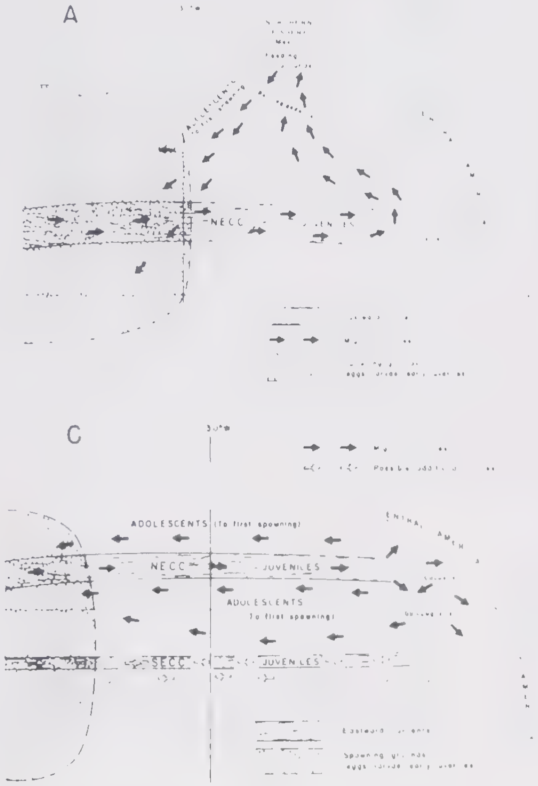
A
NECC
B
SPENT RECOVERING
C
ADOLESCENTS (To first spawning)
NECC
JUVENILES
ADOLESCENTS
To first spawning
SECC
JUVENILES
Possible additional
Eastward currents
Spawning grounds
eggs, larvae, early juveniles

Figure 39C.—Schematic representation of gyral migration model: A) routes of young skipjack tuna into the northern fishery, B) routes of adult skipjack tuna of northern fishery, and C) routes of young skipjack tuna into the southern fishery. See Figure 39A for abbreviations. (From Williams 1972.)

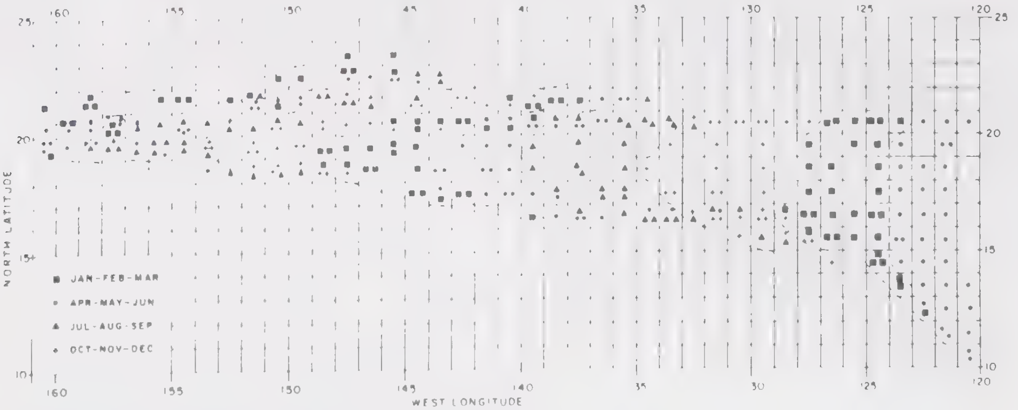

Figure 40.—Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 mo at long. 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter (from Seckel 1972).

Table 13.—Recapture data for skipjack tuna tagged by IATTC from 1960 to 1976 (from Josse et al. 1979).

Date		Days at liberty	Position		Fork length (cm)		Tag number
Recapture	Tagging/release		Recapture	Tagging/release	Recapture	Tagging/release	
6/12/62	9/05/60	646	Hawaii	Baja California	77.4	—	—
8/22/62	4/17/60	848	Hawaii	Revillagigedo Island	78.0	—	—
4/05/63	9/22/61	561	Christmas Island	Baja California	70.0	—	—
6/27/67	6/05/65	753	Hawaii	Revillagigedo Island	81.4	45.0	—
7/21/70	11/06/69	258	Hawaii	Clipperton	70.3	66.0	—
8/08/70	11/06/69	276	Hawaii	Clipperton	71.5	65.0	—
9/01/76	7/06/75	422	Molokai	Baja Magdalena, Calif.	72.7	59.0	J5242
9/01/76	7/20/75	408	South of Pearl Harbor	Cabo San Lucas, Calif.	75.1	45.0	J8250
8/22/76	7/06/75	410	Lat. 21°14′N, long. 171°51′W	Lat 24°07′N, long. 113°45′W	80.0	65.0	J5543
12/09/76	5/17/76	206	Waianae, Oahu	Lat. 31°57′N, long. 159°12′E	68.0	42.0-59.0	None
6/10/77	6/17/76	357	Kahuku, Oahu	Lat. 21°16′N, long. 111°04′W	73.0-75.0	46.0	K4105
6/28/77	6/18/76	375	Kaneohe, Oahu	Lat. 21°07′N, long. 111°16′W	76.0	53.0	L0263
7/26/77	10/04/76	295	Kaneohe, Oahu	Lat. 25°45′N, long. 112°47′W	72.3	44.0	L0222
7/29/77	6/17/76	407	Kaneohe, Oahu	Lat. 21°16′N, long. 111°04′W	75.0	47.0	K7250
8/19/77	6/18/76	427	Hawaii	Lat. 21°07′N, long. 111°16′W	74.9	47.0	L0047
9/14/77	6/17/76	454	Barbers Point, Oahu	Lat. 21°16′N, long. 111°04′W	76.0	43.0	K7182
9/20/77	6/17/76	460	Waianae, Oahu	Lat. 21°16′N, long. 111°04′W	75.2	49.0	K8615

Recaptured by a Japanese vessel.

Tagged by Japanese fishery scientists.

tuna in the Pacific, a western and an eastern central subpopulation, and two groups of skipjack tuna within the western Pacific subpopulation, an A group, derived from spawning in the northern winter, and a B group, derived from spawning in the northern summer. The migratory paths of these groups (Fig. 5) are clearly restricted to the western Pacific west of long. 170°E and the migratory paths in Japanese coastal waters agree with the paths proposed by Kawasaki (1955a, b).

In the western equatorial Pacific intensive tagging of skipjack tuna has been carried out in recent years by the Tohoku RFRL (Japan), the Department of Agriculture, Stock and Fisheries (Papua New Guinea), and the Far Seas Fisheries Research Laboratory (Japan). Preliminary analyses of tag recoveries have revealed considerable poleward migration of skipjack tuna within the boundaries of long. 130° and 160°E with none being captured farther east than long. 173°E (Kearney 1975). For the Papua New Guinea area, Lewis (1980) reported that the essential features of migration were the interchange of skipjack tuna between the Bismarck and Solomon Seas during November-April and the northerly movement from the Bismarck Sea in the July-October period. Long-term recoveries (fish 60-390 d at large) in other southern and western Pacific areas indicate straight-line migrations in excess of 1,000 mi (South Pacific Commission 1981). Fish tagged off New South Wales, Australia, were recovered in the Solomon, Samoa, and Society Islands, Kiribati, and northern New Zealand; fish tagged off northern New Zealand were recovered in West Samoa, Loyalty, and Society Islands; fish tagged off Tuvalu were recovered in the northwestern Hawaiian Islands and near Palmyra Island; fish tagged north of New Ireland were recovered in Kiribati and the Marshall Islands; and fish tagged off Volcano Island were recovered in Kiribati (South Pacific Commission 1981, Fig. 6). While straight lines connecting tag release and recovery points do not necessarily represent the actual paths of the fish, the net movement of fish from the south equatorial Pacific to the North Pacific and vice versa is significant.

Migrations of skipjack tuna have been examined on a wider scope in the Pacific. Kasahara (1968) cited Naganuma,[11] who postulated several migratory routes of skipjack tuna (Fig. 41), based on the catch as well as monthly length fre-

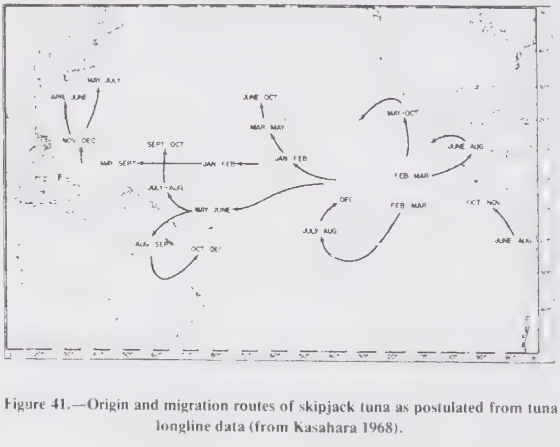

Figure 41.—Origin and migration routes of skipjack tuna as postulated from tuna longline data (from Kasahara 1968).

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[11] Naganuma, A. Unpubl. manuscr. Tohoku Regional Fisheries Research Laboratory, Shiogama City, Miyagi Prefecture, Japan.

quencies of skipjack tuna taken in the tuna longline fishery. Matsumoto (1974, 1975), on the basis of tuna longline catch data for four successive years (1964-67), proposed that there are a number of semi-independent stocks of skipjack tuna in the Pacific Ocean and that these stocks migrate in roughly circular paths (Fig. 42). The migratory paths were shown to follow a clockwise direction in the central and western North Pacific, and counterclockwise in the eastern North Pacific and in the Southern Hemisphere, corresponding with the flow of surface currents of the major water masses. By following the movement of high catch rate cells by quarters over several successive years, Matsumoto (1975, Fig. 12) has shown the probable routes by which fish can move from one area to the next and from the eastern to the western Pacific in the Northern Hemisphere and vice versa in the Southern Hemisphere within a period of 2 or more years.

Long distance migrations recorded for skipjack tuna in the Pacific Ocean are shown in Figure 43. The migrations are shown as straight-line movements between tagging and recapture sites, and do not necessarily reflect the actual paths taken by the fish in migrating from one point to another, nor the time required to negotiate the distances. Nevertheless, most of the midoceanic movements reflect the routes proposed by Matsumoto (1975).

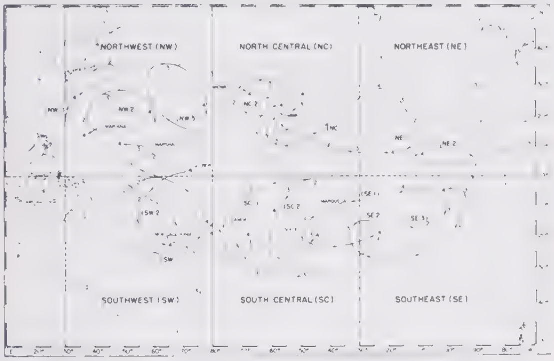

Figure 42.—Movement of the various geographic stocks of skipjack tuna in the Pacific Ocean. The numerals along the migratory routes represent quarters and locations of high catch-per-effort cells of skipjack tuna taken by the Japanese longline fishery, 1964-67. Stock designations are shown in parentheses (from Matsumoto 1974).

Local movements of skipjack tuna have been studied by tracking fish tagged with ultrasonic transmitters. A small skipjack tuna (44 cm) tracked for 8 d in Hawaiian waters by Yuen (1970), made nightly journeys of 25-106 km away from a bank and, with one exception, returned to the bank each morning (Fig. 44A, B, C). On the one exception, the fish was 9 km short of the bank; however, it remained there all day and returned to the bank on the following morning (Fig. 44D, E). The movement of the tracked fish was typical of fish which frequented the banks for feeding. Because of the repeated returns to the same spot and their consistent arrival times, Yuen suggested that skipjack tuna can navigate and that they are able to sense the passage of time.

In another study, one small (ca. 45 cm) and three large (ca. 70 cm) skipjack tuna were tagged with ultrasonic transmitters

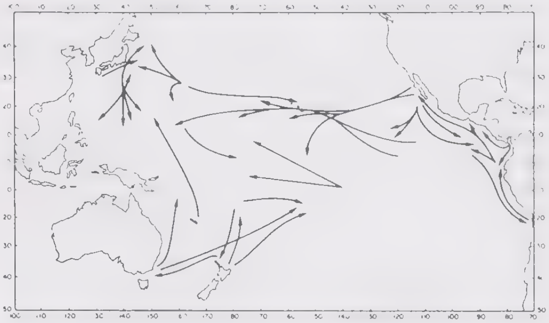

Figure 43.—Some long distance migrations of tagged skipjack tuna in the Pacific Ocean (from Forsbergh 1980).

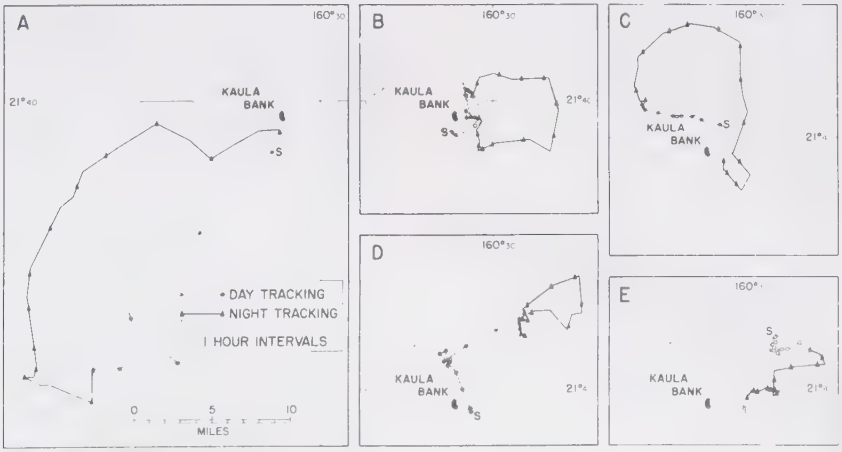

Figure 44.—Track of tagged skipjack tuna at Kaula Bank, Hawaii: (A) from 2:52 p.m., 30 August, to 6:00 a.m., 31 August; (B) from 6:00 a.m., 31 August, to 6:00 a.m., 1 September; (C) from 7:38 a.m., 3 September, to 6:00 a.m., 4 September; (D) from 6:00 a.m., 4 September, to 6:00 a.m., 5 September; (E) from 6:00 a.m., 5 September, to 7:30 a.m., 6 September (from Yuen 1970).

and tracked (Dizon et al. 1978). Behavior of the small skipjack tuna was identical to that in Yuen's (1970) study. Behavior of the larger fish, however, seemed independent of the banks. Movement during the day was characterized by many rapid vertical excursions superimposed on horizontal movement. The three fish traveled 142 km in 24 h, 50 km in 11 h, and 25 km in 10 h.

3.52 Schooling

It is well known that the skipjack tuna have a strong tendency to form schools; yet, very little is known about the mechanism involved in schooling nor the reasons which compel the species to school. Sette (1950) suggested that schooling of predators may assist in the capture of prey, whereas Breder and Halpern (1946) discussed the possibility that schooling may confer some protection from predation. Brock and Riffenburgh (1960), in treating the predator-prey relationship quantitatively, also were of the opinion that schooling of fish is a mechanism for protection against predation. The study of the courting behavior of skipjack tuna (Iversen et al. 1970) suggests yet another factor contributing to schooling. These studies, thus, point to at least three basic biological phenomena that could be responsible for causing fishes, including skipjack tuna, to school.

(1) Types of schools

Over the years, skipjack tuna schools of various kinds (in appearance) have been observed by pole-and-line and purse seine fishermen. The schools have been categorized in various ways: 1) By their association with birds, drifting objects, sharks, whales, or other tuna species; 2) by their behavior at the surface, such as milling, breezing, jumping, or feeding; and 3) by a combination of 1 and 2. The following list includes the various types of schools likely to be encountered in the oceans:

- Schools unassociated with birds
  - Milling or swirling in slow circular paths
  - Breezing or traveling
  - Jumping
- Schools associated with birds or bird flocks
  - Same as above
- Schools associated with drifting objects
- Schools associated with sharks
- Schools associated with whales

Among these, the last three types may be accompanied occasionally by birds or bird flocks, and all types could be of either pure or mixed school, i.e., schools made up entirely of skipjack tuna or mixed with other tuna species or other fishes.

Schooling behavior is relatively easy to observe at the surface, but such is not the case of fish beneath the surface. There is ample evidence that the skipjack tuna also school at depth. Schools of skipjack tuna have been recorded on the echo sounder at depths from 20 to 150 m (Kimura et al. 1952) and from 25 to 200 m (Iwasaki and Suzuki 1972). Strasburg et al. (1968) reported seeing a school of approximately 250 skipjack tuna at depths over 90 m from a small submarine.

(2) Associations

The association of birds with tuna schools is based on a common interest in the same concentration of prey. Birds were observed to follow tuna schools and to prey upon small fish chased to the surface by the schools (Godsil 1938; Royce and Otsu 1955). Since birds are more readily seen at a distance than fish schools, it is not surprising that the majority of skipjack tuna schools sighted are those accompanied by birds (Kimura 1954).

Skipjack tuna are frequently sighted at sea in the presence of other tunas (Orange et al. 1957; Broadhead and Orange 1960; Waldron 1963), with logs (Uda and Tsukushi 1934; Imamura 1949; Yabe and Mori 1950; Kimura 1954; Kuroda 1955; Inoue et al. 1963, 1968a, b; Hunter and Mitchell 1967); rafts (Kojima 1960; Gooding and Magnuson 1967; Murdy 1980; Aprieto 1981; Matsumoto et al. 1981); other flotsam, such as ship's material, airplane fuel tanks, carcasses of dead whales, etc. (Inoue et al. 1963); and sharks (Uda 1933; Godsil 1938; Imamura 1949; Kimura 1954; Kuroda 1955; Tominaga 1957). The occurrence of these associations vary markedly with geographical area and time of year (Uda 1933; Uda and Tsukushi 1934; Kimura 1954). Uda (1933) reported that, in the western Pacific Ocean, skipjack tuna schools associated with birds, whales, or logs generally appear in greatest number in the main Kuroshio system in May and June, whereas schools associated with sharks appear for the most part in warm water pockets where the Kuroshio and Oyashio systems impinge upon each other in July and August.

The occurrence of mixed schools containing skipjack tuna and other tuna species is relatively common. In the eastern Pacific Ocean, Orange et al. (1957) and Broadhead and Orange (1960) reported that 72 and 62% of the yearly catches of skipjack tuna by purse seiners and bait boats, respectively, were made from pure schools, or conversely, 28 and 38%, respectively, from mixed schools. Kawasaki (1959, 1965a) reported that aside from mixed schools containing yellowfin tuna, fish species most frequently found with skipjack tuna are the kawakawa, frigate tuna, bluefin tuna, albacore, bigeye tuna, and dolphin. Yabe and Mori (1950) reported other fishes, including wahoo, *Acanthocybium solandri*; rainbow runner; amberjack, *Seriola intermedia*; triggerfish, *Canthidermis rotunadatus*; and jack, *Caranx equula*, are taken along with skipjack tuna associated with driftwood in waters off southern Japan. However, it is doubtful whether these fishes were truly mixed with the skipjack tuna schools per se.

Associations of fishes with floating objects have been studied by a number of workers. While protection from predators or availability of food was given as the reason for attraction by some (Hardenberg 1950; Kojima 1956; Soemarto 1960; Gooding and Magnuson 1967), food was considered unimportant by others (Yabe and Mori 1950; Senta 1966). The importance of shade was discounted by all. As for the skipjack tuna, Gooding and Magnuson (1967) found them to be transients. Hunter and Mitchell (1967) found little evidence to support the mechanisms postulated by others, i.e., attraction to food, response to shade, shelter from predators, presence of spawning substrate, and parasitic-cleaning symbiosis. They suggested two mechanisms: 1) That the objects function as schooling companions and 2) that for fishes not adapted to pelagic life, the objects function as substitutes for reef or substrate.

Uda (1933) stated that skipjack tuna congregate around whale sharks (Rhinodontidae) in fear of spearfish. Tominaga (1957) also reported that skipjack tuna associate with basking sharks (Cetorhinidae) for protection from marlin. The latter's observations of this relationship indicate that the shark is the likely leader and the skipjack tuna the followers, and that the attachment of the skipjack tuna to the shark is quite strong. The skipjack tuna "swim in front, behind, to the sides, above, and below the shark. When attacked by a spearfish, the skipjack close in toward any part of the shark's body. Upon chumming such a school, the skipjack will come toward the bait, but if the shark moves away from the ship, the skipjack will proceed after the shark immediately."

Association of skipjack tuna with whales may also be for protection, but is not as close as that with sharks (Tominaga 1957). According to Tominaga, the association usually occurs with one or two whales, seldom with a herd. When attacked by marlin, the skipjack tuna merely comes in the vicinity of the whale. In this association, the skipjack tuna always precede the whale and may abandon the whale while the school is being fished.

Skipjack tuna are found associated also with anchored floating objects. Fishing for tunas around such objects (bamboo rafts) has been done for many years in the Philippines, where tuna were caught by hook and line (Murdy 1980). The introduction of purse seiners in the early 1960's (Aprieto 1981) and the rapid development of techniques for purse seining around the rafts have resulted in a highly successful commercial fishery for tunas (Matsumoto[12]). Recent experiments with fish aggregating devices constructed of two 55-gal steel drums and moored in depths of 400-2,200 m in waters around the Hawaiian Islands have been successful in attracting skipjack tuna and other tuna schools in sufficient quantities for commercial pole-and-line fishing (Matsumoto et al. 1981). Similar experiments are being conducted by several island states in the South Pacific and in the Indian Ocean.

(3) Distribution of types of schools

The distribution of the various types of schools differ by area and time. In the northwestern Pacific Ocean, off northeastern Japan, Uda (1933) reported that skipjack tuna schools associated with birds, whales, or logs generally appeared in greatest number in the main Kuroshio system, while schools associated with sharks appeared for the most part in warm water cells where the Kuroshio and Oyashio impinged upon each other. He also noted that schools associated with whales were seldom found in the southern portion of the Kuroshio. Kimura (1954), in a more extensive study off northeastern Japan, obtained additional details: 1) Schools unaccompanied by birds were more often found at the boundaries of the Kuroshio and Oyashio, 2) schools associated with sharks also occurred in warmer waters slightly south of the two current boundaries, and 3) schools associated with birds were seldom seen in offshore waters (ca. 800 km). He further determined the percent occurrence of the various types of schools and plotted the average occurrence of the three most common types of schools in the area (Fig. 45). Schools associated with birds were abundant in May and June but were relatively scarce during the peak of the season, July to September. Schools associated with sharks first appeared in early June, were predominant in July, and disappeared in October. Schools unaccompanied by birds were abundant in August and September and predominant in October.

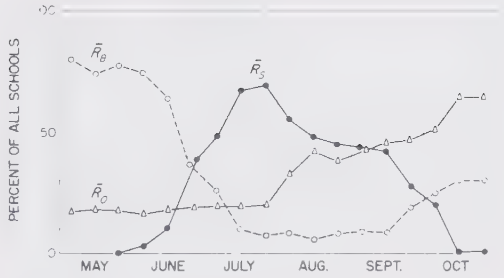

Figure 45.—Ratio of detection of schools with birds ($\bar{R}_B$), schools without birds ($\bar{R}_O$), and schools with sharks ($\bar{R}_S$) to total schools in each 10-d period (from Kimura 1954).

In more southern areas west of the Bonin Islands (lat. 19°-24°N, long. 136°-147°E), schools associated with whale sharks have been reported in October and schools associated with logs in February (Tohoku Regional Fisheries Research Laboratory undated a). Further south, in the area lat. 2°-5°N, long. 134°-150°E, schools associated with logs and bird flocks regularly occurred from December through February. Lastly, in waters south of the Equator, around Papua New Guinea and the Solomon Islands, schools were generally associated with bird flocks, with few instances of association with sharks or logs (Tohoku Regional Fisheries Research Laboratory undated b, d). Living Marine Resources (1977), however, reported that numerous logs of all sizes from twigs to entire trees were sighted and fished by three U.S. purse seiners in August-October 1976 in the area northeast of Papua New Guinea (lat. 3°N-4°S, long. 138°-154°E) in the South Equatorial Current. More specifically, T. K. Kazama[13] reported few log sightings in the area lat. 8°-3°N, long. 147°E, but that sightings increased considerably to the south (lat. 2°-4°S, long. 138°-147°E), numbering several hundred per day with the greatest single concentration of logs extending over an area approximately 15.5 m (50 ft) wide and 1.8 km (1 mi) long.

A vastly different situation prevails in the central Pacific Ocean, where almost all of the fish schools sighted are accompanied by birds. Murphy and Ikehara (1955) observed that about 85% of all fish schools sighted in waters around and between the Hawaiian, Line, and Phoenix Islands were accompanied by birds. Likewise, for two scouting cruises around the Hawaiian Islands during the spring of 1953, Royce and Otsu (1955) reported that every one of 253 fish schools sighted was accompanied by birds. Undoubtedly, this dependence on bird flocks for finding tuna schools in the central Pacific Ocean arises from the prevalence of birds in the area and partly from the prevailing sea state, which is commonly choppy, with numerous white caps. The latter condition makes it extremely difficult to see the wake of a school or jumping fish at any appreciable distance from a vessel. Schools associated with sharks, whales, or logs were not mentioned in either report. The absence of such schools is as expected since one of the sharks normally associated with skipjack tuna, the basking shark, is not found in these waters and to date there has been only a single report of the other, the whale shark, in Hawaiian waters (Gosline and Brock 1960). Drifting logs also are encountered only sporadically (personal observation by the senior author) in Hawaiian waters.

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[12] Matsumoto, W. M. Purse seining around payao in the Philippines. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812

[13] Kazama, T. K. 1976. Report on observations made aboard one of three purse seiners chartered by Pacific Tuna Development Foundation to fish in the western equatorial Pacific. Admin. Rep. 8H, 7 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812

A report by Waldron (1964) summarized skipjack tuna schools and bird flocks observed in an area of the central Pacific Ocean bounded by lat. 30°N-20°S and long. 110°W-180° during 128 cruises by vessels of the U.S. National Marine Fisheries Service, Honolulu Laboratory, between 1950 and 1961. The results (Fig. 46) indicate that 1) high rates of sightings of both skipjack tuna schools and bird flocks were most prevalent in time-area units containing island groups, 2) there were distinct seasonal changes in sightings between island groups, and 3) the rate of sightings in the Marquesas Islands area was much higher than for other areas of similar size.

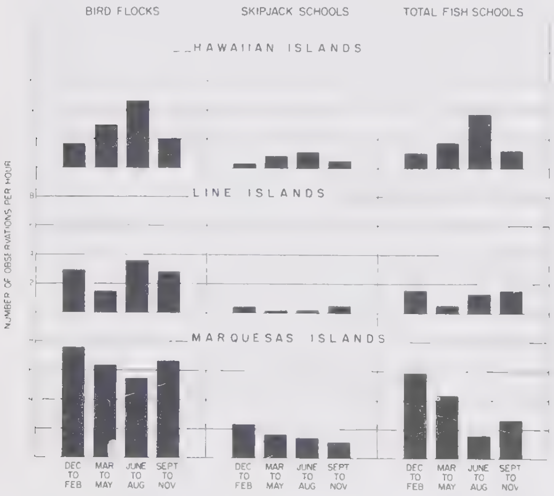


Figure 46.—Seasonal variation in rate of bird flock, skipjack tuna schools, and total fish school sightings for three major island groups (from Waldron 1964).

(4) Length distribution of schools

Brock (1954) noted a comparatively small range of lengths within individual schools in the Hawaiian fishery, in contrast to the range of lengths in the landings as a whole. The mean range of lengths for single school samples was 11.3 cm, with 5 and 21 cm being the least and greatest, whereas the range for the seasonal landing was 47 cm. He thus concluded that the skipjack tuna school was highly size-selective and hypothesized that the segregation by size was likely due to the maximum swimming speed attainable by fish of the same size.

Based on observations from the eastern Pacific tuna fishery, Schaefer (1948) suggested that the tendency of tunas to aggregate by size might, in some cases, be stronger than the tendency to aggregate by species. In addition, Broadhead and Orange (1960) observed that the frequency distributions of the lengths of skipjack tuna in pure and mixed species schools were similar, whereas those of yellowfin tuna differed noticeably (Fig. 47).

Kawasaki (1964) compared length-frequency distributions of skipjack tuna taken from various types of schools in Japanese waters and noted that the variations in length within each school type increased in the following order: pure school (without birds), bird-associated school, whale-associated school, shark- or driftwood-associated school. Although Kawasaki's classification of pure- and bird-associated schools is confusing, a pattern is discernible here, i.e., the less mobile the object of association, the greater the size range of fish associated with it. This observation is, thus, consistent with Brock's (1954) hypothesis, since schooling under slow moving objects does not require uniform maximum swimming ability.

Catches of tunas from under stationary floating objects further support Brock's hypothesis. Matsumoto (footnote 12) observed that purse seine catches beneath anchored bamboo rafts in the Philippines included tunas (skipjack, yellowfin, and bigeye tunas, kawakawa, and frigate and bullet tunas) ranging widely in sizes from 24 to 63 cm. One or two large yellowfin tuna or bigeye tuna, 30 to 70 kg or more. were also taken occasionally.

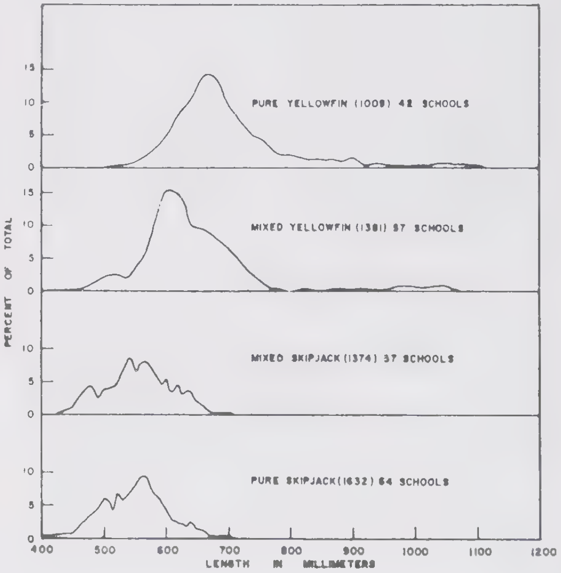


Figure 47.—Frequency distributions of lengths of yellowfin tuna and skipjack tuna from schools of pure and mixed-species composition sampled from bait vessel catches (from Broadhead and Orange 1960).

(5) Size of school

Estimation of school size has been attempted in the eastern Pacific Ocean by Orange et al. (1957), based on the catch-per-set by purse seine vessels, and by Broadhead and Orange (1960), based on the catch-per-school by bait boats. Estimates based on purse seine catches were considered more reliable than those based on bait boat catches because it is assumed a greater percentage of a school is taken by seining than by baitfishing. However, actual school sizes would still be greatly underestimated, since entire schools are not always caught by the purse seine (Orange et al. 1957).

The frequency distribution of catch-per-successful set by species composition categories plotted by Orange et al. (1957) showed that the distributions of pure skipjack tuna schools were skewed very strongly toward small catches (Fig. 48), with more than 50% of the sets falling in the two smallest size classes, i.e., 0.25-4.9 and 5.0-9.9 tons. (Note: Orange et al. used short tons.) The average catch-per-set of pure skipjack tuna schools in the eastern Pacific for the 4-yr period studied was 13.5 tons, with a range of 1 to 130 tons (from their table 2). Along the northeastern coast of Japan, the average catches-per-successful set of one-boat and two-boat purse seine vessels were 6.3 and 8.6 tons, respectively (Inoue 1959). Either the schools in the eastern Pacific were larger than those in waters off Japan, or the fishing environment and technique were more conducive to greater catches from similar-sized schools in the eastern Pacific. It is also possible that seiners in the eastern Pacific are less apt to set on small schools than seiners off Japan. On the basis of Figure 48, one can say that the occurrence of small schools (<20 short tons) was the rule and that large schools over 50 short tons occurred less frequently.

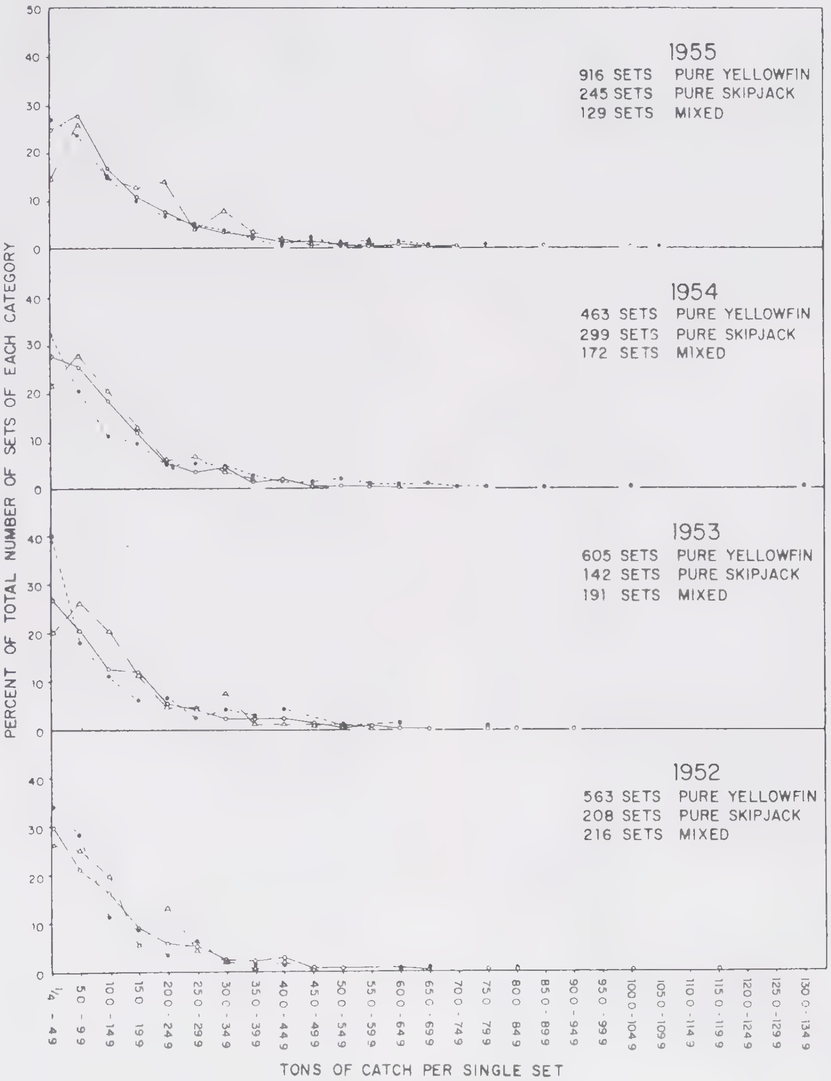


Figure 48.—Percentage frequency distributions of catch-per-set in the eight principal fishing areas of the eastern Pacific tuna fishery, for each year 1952 through 1955, by species-composition categories. Open circles represent catches of pure yellowfin tuna. Solid circles represent catches of pure skipjack tuna. Triangles represent catches of mixed species (from Orange et al. 1957).

The frequency distribution of catch-per-school from pole-and-line fishing (Broadhead and Orange 1960), was similarly skewed strongly toward the small catches (Fig. 49). The majority of the catches (about 65%) from pure schools fell into the two smallest size categories, 0.5 and 1.5 tons (note: Broadhead and Orange used short tons), and the mean catch for all schools was 2.8 tons. The difference in the mean catches by bait boats (2.8 tons) as compared with that of purse seine vessels (13.5 tons) probably reflects lower efficiency of pole-and-line fishing and the likelihood that the purse seine vessels may shun small schools more often than pole-and-line boats.

Broadhead and Orange (1960) compared the sizes of schools fished in the eastern Pacific and Hawaiian fisheries by plotting the distribution of catches from the two areas. Data from the Hawaiian bait boat catches yielded a J-shaped curve similar to that of the eastern Pacific catches but the points fell well below that of the latter. The mean catch-per-school was about 1 ton compared with 2.8 tons from schools fished in the eastern Pacific Ocean. On the basis of this comparison, they stated, "It appears that the skipjack tuna schools fished in the Eastern Tropical Pacific area are, on the average, somewhat larger than those fished in the vicinity of the Hawaiian Islands (assuming that the bait vessels capture the same percentage, on the average, of each school encountered in the two regions)." Such a comparison, however, is dubious since their assumption is incorrect. Both vessel size and number of men fishing per boat differ greatly between the two fisheries, thus resulting in disproportionate catches.

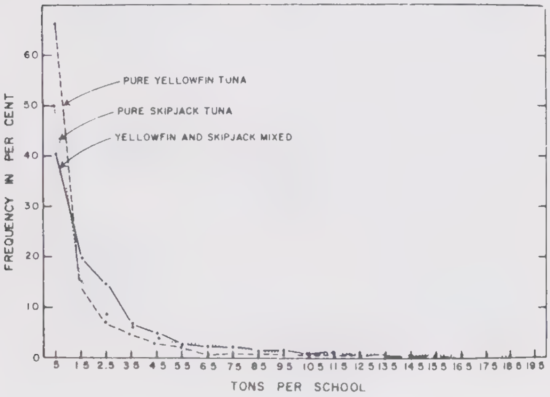


Figure 49.—Percentage frequency distributions of catch-per-school (tons) by bait vessels, by category of school, 1956-58 (from Broadhead and Orange 1960).

(6) Schooling at night

Some evidence for skipjack tuna schooling at night is available in the literature. Nakamura (1962) observed that skipjack tuna in captivity swam slowly about the perimeter of the pool, often with their bodies normal to the light rays from the floodlight. Fish were observed once at night without the floodlight. On this occasion (moonlight was sufficient to allow the fish to be seen), the fish remained in a school and swam slowly around the pool. Other evidence of schooling at night comes from Yuen (1970). While tracking skipjack tuna fitted with ultrasonic tags, he observed that a school of skipjack tuna was often visible at the position of the tagged fish. On several occasions, both day and night, switching the sonar to the active mode disclosed many fish targets in the vicinity of the tagged fish.

(7) Activity of schools

That schooling occurs at depths in excess of 100 m was shown by Kimura et al. (1952) and Iwasaki and Suzuki (1972). From vessels equipped with echo sounders, Kimura et al. (1952) located fish schools between depths of 20 and 150 m. They identified them as skipjack tuna by tracking them on the echo sounder and fishing them as they reached the surface. In some instances chumming with baitfish caused the schools to rise to the surface from depths as great as 100 m within 45 sec, a speed of 2.2 m/s (4.3 kn).

Underwater observations of skipjack tuna schools by Strasburg and Yuen (1960), Strasburg (1961), and Yuen (1970) provide further insight into the behavior of skipjack tuna schools. Strasburg and Yuen (1960) observed that the activity of schools varied with fish size. First, small skipjack tuna (ca. 20 cm) schooled in large numbers (in the thousands), and in spite of their size, the schools seemed to respond instantaneously to stimuli. The fish were closely spaced and maneuvered with precision. Even during feeding, these schools never entirely lost their integrity. Second, in schools of medium-sized fish (45-65 cm), feeding activity was frenzied and most semblance of schooling was lost. The fish made rapid dashes to the surface at speeds of about 12.9 m/s (25 kn), either singly or in pods of half a dozen or so; hence, their swimming was seldom horizontal but oscillated vertically in patterns resembling a series of sine curves. Third, schools of large skipjack tuna (70-80 cm) appeared lethargic in comparison with schools of smaller fish. There were no signs of schooling during feeding, and the individual fish never appeared to swim faster than about 5.1 m/s (10 kn). More often the fish cruised at 1.0 to 2.1 m/s (2 to 4 kn), swimming nearly horizontally, with surface dashes being relatively unhurried.

Strasburg and Yuen (1960) also noted that 1) water sprayed on the surface while chumming increased feeding frenzy, resulting in increased catches, 2) fast chumming (twice normal) resulted in decreased catches, 3) slow chumming or insufficient bait caused the fish to scatter and reform into schools away from the vessel, resulting in decreased catches, and 4) neither sound, blood, or skin extracts appeared to have much effect on actively feeding schools.

One other school activity was observed by Strasburg (1961). During experimental fishing in Hawaiian waters, he noted that a school being fished would abruptly dive vertically and vanish from view. Examination of stomach contents of fish from such schools showed that they had consumed postlarval *Synodus variegatus* and juvenile *Holocentrus lacteoguttatus*, both reef-type fishes, and that the occurrence of these fishes in the stomachs was significantly related to diving frequency. Observations on the number of diving schools indicated that diving was the rule rather than the exception. The number of dives per school ranged from 0 to 8 (Fig. 50) with a mean of 2.7. The schools were away from the surface as briefly as 3 s or as long as 28 min. In a later study (Strasburg et al. 1968) reef-type fishes, such as those found in the stomachs above, were observed from a small submarine at depths of 107 to

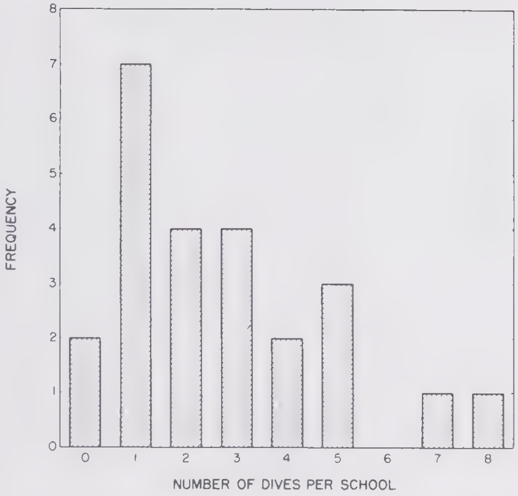


Figure 50.—Frequency of diving in Hawaiian skipjack tuna schools (from Strasburg 1961).

192 m, suggesting that skipjack tuna schools may have descended to these depths to feed.

(8) Biting response of schools

The factors influencing the biting response of skipjack tuna schools have been studied by a number of scientists. These factors include (a) state of hunger, (b) behavior of prey, (c) condition of gonads, (d) distance from land, (e) time of day, and (f) weather.

(a) State of hunger, as determined by the amount of food in the stomachs

Uda (1933), Suyehiro (1938), and Hotta et al. (1959) noted that skipjack tuna responded to bait well when their stomachs were empty, and poorly when full. Uda (1933) further observed that skipjack tuna with stomachs between the extremes of fullness and emptiness tended to respond more poorly than when their stomachs were emptier. This statement, however, is contrary to Yuen's (1959) observation that skipjack tuna schools responded to bait longer when the major food items in the stomachs were in the earlier stages of digestion and that the response became greater as the stomachs emptied. Similarly Uda's (1933) statement is contrary to Magnuson's (1969) observation that attacks by captive skipjack tuna on food particles decreased rapidly only after the stomach contents exceeded 50% of the stomach's capacity.

(b) Behavior of prey

Skipjack tuna feeding on fast-swimming fishes such as tunas, carangids, and gempylids, exhibit a more favorable biting behavior than skipjack tuna feeding on slower swimming chaetodontids, scorpaenids, molids, and acanthurids (Yuen 1959).

(c) Condition of gonads

Brock (1954) commented on the rarity of skipjack tuna with fully ripe gonads and the lack of spawned-out ovaries within the spawning season in his extensive sampling of fish in the Hawaiian skipjack tuna fishery. He suggested that fish with ova larger than 0.7 mm in diameter become progressively less available to the fishery. This suggests that female skipjack tuna may abstain from feeding, immediately prior to and during the spawning period. Yuen (1959) found that maturation of the ovary did not appear to affect biting response, except in fish with ripe eggs. That skipjack tuna likely undergo a period of fasting is borne out by fishermen's remarks (see Section 3.41(4)) concerning the futility of fishing such schools.

(d) Distance from land

Suyehiro (1938) measured biting quality by catch rate (number of fish per man per 100 min), designating a catch of 16 or less fish as poor biting and 17 or more fish as good biting. Applying this criteria to schools fished in Japanese waters by 17 vessels, he found that skipjack tuna schools around islands bit poorly, whereas schools in the open sea generally bit well. Yuen (1959) reported a similar relationship; however, this was true only for large (>60 cm) fish.

(e) Time of day

Uda (1940) reported that there is a relation between time (hour of catch) and total catch, as well as between time and catch-per-school. He observed that catches peaked three times during the day, a primary peak between 0500 and 0900, a secondary peak between 1200 and 1300, and a tertiary peak between 1600 and 1800; and that about half of the day's catch was made between 0500 and 0900, and about two-thirds of the day's catch prior to noon. He explained the pattern of catch thusly: "The fish school and feed most actively in the early morning, and once their stomachs are filled their appetites decline, but around noon, for reasons connected with the time required for digestion, their appetites again increase and they become slightly active." He believed that the decrease and increase in appetite occurred again in the evening just before sunset. While his explanation above agrees with the results obtained by Magnuson (1969) from feeding experiments conducted on skipjack tuna in captivity (see Section 3.41(4)), similar peaks were not reflected in the catch rates shown in 2 of the 4 yr he examined.

A similar study was done in the central Pacific by Uchida and Sumida (1971), but rather than using catch and catch rates as the variables, they used number of schools sighted and number of schools fished successfully. These variables plotted against time of day (Fig. 51) resulted in curves not unlike that obtained by Uda (1940); however, their interpretation of the curves differed. Fishing success (i.e., schools yielding catches) increased rapidly from daybreak to a peak at 0901-1000, dipped slightly at 1001-1100, and was followed by two peaks at 1201-1300 and 1401-1500. The authors attributed the dip at 1001-1100 to reduced scouting effort due to time taken for lunch. They suggested that the time taken for breakfast and dinner also may have partly affected the

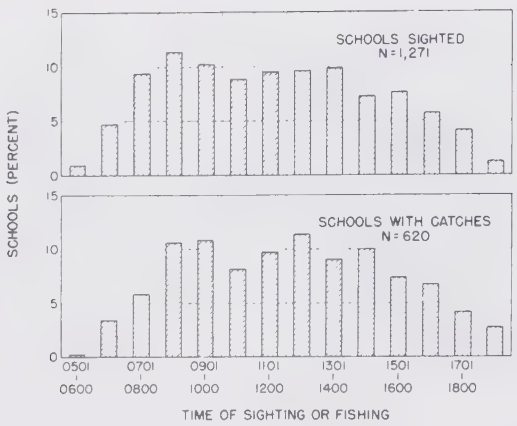


Figure 51.—Frequencies of school sightings and schools with catches, by time of day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967 (from Uchida and Sumida 1971).

reduced sightings and catches near sunrise and sunset. Additionally, unlike the Japanese fishery, where most of the day's catches were made prior to noon, most of the day's catch in the Hawaiian fishery occurred after midday (Table 14).

Table 14.—Percentage of the day's total catch aboard the vessels in the first (by 0900), second (0901-1200), third (1201-1500), and fourth (after 1501) quarters of the fishing day for seven Hawaiian skipjack tuna fishing vessels, June-August 1967 (from Uchida and Sumida 1971).

	Quarters of the fishing day			
Vessels	First	Second	Third	Fourth
A	3.3	31.5	42.4	22.8
B	15.5	15.3	35.4	33.8
C	17.0	20.2	23.7	39.1
D	9.2	24.9	35.2	30.7
E	7.1	41.6	28.5	22.8
F	7.2	40.9	33.3	18.6
G	16.4	10.3	21.0	52.3
All	10.8	26.4	31.4	31.4
Cumulative	10.8	37.2	68.6	100.6

(f) Weather

To what degree weather affects the biting behavior of skipjack tuna schools has not been clearly determined. Suyehiro (1938) reported that in the western Pacific Ocean biting seemed to be better in cloudy than in clear weather, and that biting appeared equally good in rain and fog as in clear weather. He noted, however, that the reliability of the latter was questionable due to few data. He also reported that wind velocity was not related to biting quality. In the central Pacific Ocean, Yuen (1959) observed that weather conditions were predominantly uniform and biting behavior did not change by much. On a few days darker than usual, the weather affected fishing only in decreasing the chances of sighting schools.

(g) Other aspects of biting behavior

In the western Pacific Ocean, Uda (1940) indicated that in most of the schools fished, catches generally occurred between 10 and 40 min of fishing, that the catch rate (catch-per-school) increased in direct proportion to the increase in fishing time up to 80 min, and that when fishing time exceeded 80 min, neither the total catch nor the catch rate showed any increase. Similarly, in the central Pacific Ocean, fishing duration of most schools was between 5 and 40 min (Yuen 1959; Uchida and Sumida 1971) and the catch-per-school increased proportionally with fishing duration (Fig. 52).

Yuen (1959) also measured other factors that seemed to influence catch. Of these, 1) fishing duration, 2) peak catch rate, 3) postpeak duration, 4) rate of increase of prepeak catch rates, and 5) mean number of hooks per minute were all found to be related significantly to total catch (Table 15). Of these, 2) and 3) were subsequently used as measures of skipjack tuna response, on the premise that peak catch rate would measure the degree of interest or intensity in feeding and postpeak duration would measure the duration of interest.

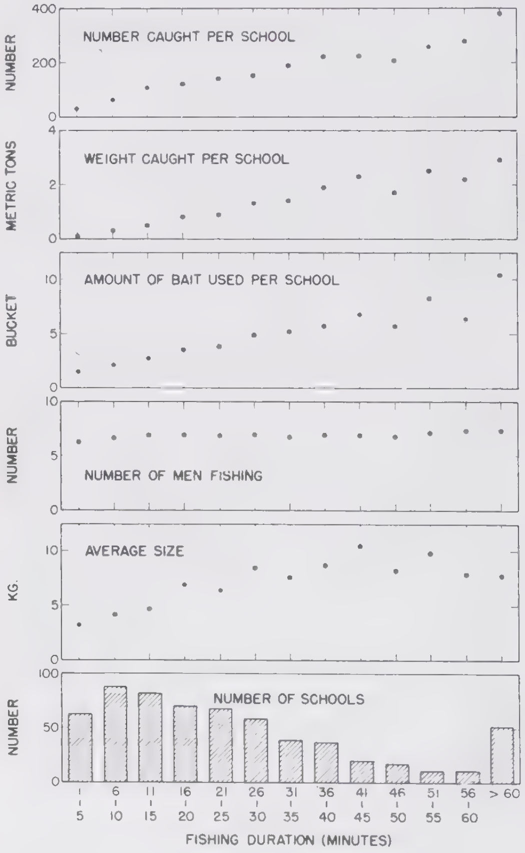


Figure 52.—Relation between fishing duration and average values of catch per school, amount of bait used per school, number of men fishing per school, and size of fish per school, June-August 1967 (from Uchida and Sumida 1971).

Table 15.—Correlation coefficients of total catch of skipjack tuna with various measures of fishing (from Yuen 1959).

Measure	df	r
Fishing duration	84	[1]0.772
Peak catch rate	84	[1]0.614
Prepeak duration	84	0.201
Postpeak duration	84	[1]0.868
Rate of prepeak increase	71	[2]0.274
Rate of postpeak decrease	73	−0.120
Mean number of hooks	84	[1]0.289
Number of passes	81	−0.06
Time from start of pass to start of fishing	79	0.01

[1] Values beyond the 1% level of significance.

[2] Values beyond the 5% level of significance.

Yao (1962) examined the biting qualities as judged and recorded on fishing reports by Japanese fishermen. In these reports biting qualities were judged as good when:

1) Fish were attracted in large numbers immediately upon chumming and there was a sudden initial increase in catch,
2) the number of fish increased beyond the fishermen's capacity to catch them,
3) the duration of fishing above a minimum catch rate was long,
4) catch per school was large, and
5) maximum catch was attained quickly.

Yao calculated the biting qualities of schools, employing Yoshihara's (1960) theory on the mechanism of skipjack tuna fishing, by the equation

$$W = N \left(1 - (1 - \lambda t)e^{-\lambda t}\right)$$

where W is the number of fish caught, t is fishing duration, N is number of fish in school, and λ is the biting coefficient expressed as the reciprocal of the length of time until the catch rate reached a maximum. Yao's calculations indicate that 1) through 4) tend to be judged higher as school size increases, even when the degree of biting was the same. Ignoring school size, he found no statistical differences in the mean biting coefficient among schools judged as good, average, and poor by the fishermen.

Yao (1962) also observed that the mean biting coefficient, 0.135, for small schools (<1,000 fish) was extremely high, as compared with the mean coefficient, 0.085, of large schools (>2,000 fish). He suggested that the high mean coefficient for small schools was due to selective fishing of only good biting schools, whereas fishing was done on both good and slow biting schools when the schools were large.

Summarizing the above, it seems that fish respond well to chum when their stomachs are less than half filled and when they are feeding on fast-swimming prey; that schools in offshore areas respond better than those inshore; that fish, particularly females, respond poorly during spawning; that the response reaches a peak in the early morning between 0800 and 1000; that there may be more than one feeding peak during the day; that the response generally lasts from 5 to 40 min, depending on school size and state of hunger; and that weather may not be a factor in influencing feeding behavior.

3.6 Physiology

3.61 Energy transfer (metabolism)

Rapid and efficient energy turnover, more than any other single biological factor, characterizes the skipjack tuna's physiological ecology. Life in the warm and relatively unproductive tropical waters necessitates elaborate adaptations for locating and efficiently utilizing the patchily distributed food resources. Studies of these adaptations and estimates of energetic rate processes have provided information and insights for modeling of important management parameters (Sharp and Francis 1976). The detailed understanding of the skipjack tuna's energy budget has had its genesis in basic biological information obtained from experiments with captive specimens at the Kewalo Research Facility of the National Marine Fisheries Service in Honolulu. Indeed, this research facility is the source of much of what is known about the basic biology of tropical tunas.

(1) Energy budget

In all animals, energy transfer in and out of the animal is quantified in the energy budget or mass balance equation (Ricker 1968):

$$C = R + U + F + G + B$$

where C = rate of food consumption
R = rate of metabolism
U = rate of excretion
F = rate of egestion
G = rate of gamete production
B = rate of growth.

For our purposes the units in the analysis of this relationship will be given in caloric units (kcal). Skipjack tuna, for instance, contain an average of 1.46 kcal/g of live weight (Kitchell et al. 1977), and the mean caloric value of skipjack tuna forage is assumed to be 1.1 kcal/g wet weight (Kitchell et al. 1978).

The rate of metabolism (R) is lumped by Kitchell et al. (1978) into two components: 1) The energy, or specific dynamic action (SDA), required to process the forage, and 2) the remainder of the metabolic work (M). Table 16 presents the energy budget values of a 1 kg skipjack tuna under six input-output levels (Kitchell et al. 1978). Values for SDA, U, and F are assumed from work on other fish to be 15, 5, and 15% of ingested calories. Thus, the energy available for M and storage as growth or gonadal development is 0.65 of the calories eaten. Input of calories in the table range from starvation, maintenance calories (no growth) of 5.9% of body weight per day, ingestion of necessary calories to produce "normal" growth (0.7% of body weight per day, Uchiyama and Struhsaker 1981) at three arbitrary multiples of activity, and maximum ingestion of 30% of body weight per day. The maximum ingestion rate was determined in laboratory studies.

Growth under these input conditions varied from −3.6% under starvation conditions to a maximum growth rate of 6.9% of body weight per day when fish were feeding at maximum rations (30% of body weight per day while maintaining levels of activity nearly three times those at minimum sus-

Table 16.—Estimated energy budget terms at six bioenergetic regimes for a 1 kg skipjack tuna at 24°C (from Kitchell et al. 1978).[1]

Bioenergetic regime	Requisite ration (% body wt./d)	Process rate (cal/kcal per day) Consumption (*C*)	Net metabolism (*M*)	SDA	Excretion (*U*)	Egestion (*F*)	Growth (ΔB)
Starvation	0	0	29	5	2	0	–36
Maintenance	5.9	44	29	7	2	7	0
Observed growth at							
1 Lab M (= Level I)	7.3	57	29	9	3	9	7
2 Lab M (= Level II)	13.1	99	58	15	5	15	7
2 Lab M (= Level III)	19.0	143	87	21	7	21	7
Maximum	30.0	250	87-155	38	12	38	7-69

[1] Daily ration is given as percentage of body weight consumed per day assuming 1.1 kcal/g live food.

tainable cruising speeds). If activity levels include metabolic costs to five times that at minimum cruising speed, growth rates would be only 0.7%/d at maximum rations. Kitchell et al. (1978) reasoned that these levels of activity were unrealistically high and, therefore, the observed growth rates of 0.7%/d indicated limited food availability rather than high levels of activity.

In skipjack tuna, unlike most other animals, the routine metabolic rate per unit of weight does not decrease as size increases (Brill 1979; Gooding et al. 1981). Large fish have approximately the same metabolic rate per unit of mass as small fish. The reasons for this phenomenon are obscure. However, in skipjack tuna, as in most other animals, the relative capacity for feeding does decrease as size increases. In absolute terms, large fish can eat more than small fish but in relative units, the maximum ration per unit of weight decreases as size increases. Ability to acquire energy and the energy costs of metabolism thus converge as skipjack tuna size increases. This interesting relationship can be used to predict the limits of growth. It has been shown that to pursue and capture prey takes a metabolic rate approximately two times the rate required to just swim at minimum speed (speed required to maintain hydrostatic equilibrium, Magnuson 1973). Then the maximum ability to provide surplus energy for growth (0.65 of maximum ration) is equivalent to the minimum activity necessary for feeding by skipjack tuna weighing 25-30 kg.

For yellowfin tuna, unlike skipjack tuna, the metabolic rate per unit weight declines as size increases. The maximum feeding rate also declines but at a slightly more rapid rate than metabolism. As in skipjack tuna, both rates converge but at levels that predict maximum yellowfin tuna sizes of 150-200 kg. The maximum predicted sizes of the two tunas can be compared with maximum sizes in Section 3.31 for skipjack tuna (22-25 kg) and the largest known yellowfin tuna (180-200 kg).

An economic analogy may help make these concepts more understandable. If: 1) feeding rate is taken as income; 2) egestion, excretion, and SDA rates as taxes (proportional to income); and 3) metabolic rate as fixed costs, then growth (somatic and/or gonadal) can be considered net profit. Small animals have the potential for large profits because their fixed costs are low and their income potential is high. As size increases, so too do fixed costs and taxes, but potential profit margin narrows due to a less rapid increase in income potential. Eventually they converge at a point that dictates the maximum size. In yellowfin tuna, in contrast to skipjack tuna, the fixed costs decline slightly (an economy of scale) as size increases, allowing it to become larger before the convergence of costs and profits occur. Obviously, any differences between real income (food availability) and maximum income potential will cause the zero-profit level to develop at a smaller size.

(2) Respiration

Intermediary metabolism is the process whereby energy is made available for biological power, the fixed costs referenced in the preceding section. Intermediary metabolism, sometimes called internal respiration, is measured in units of oxygen consumed, calories transferred, carbon dioxide liberated, or power in watts. All are stoichiometrically related. External respiration is defined as the mechanism which delivers O_2 and expels CO_2.

Since skipjack tuna cannot use buccal or opercular pumping to force water over their gills, they must continually swim or they will suffocate. They are "ram ventilators." A 44 cm skipjack tuna swimming at a basal speed of 66 cm/s, has a gill resistance equal to 7% of its total swimming resistance (Brown and Muir 1970). The cost of this extra resistance is approximately 1 to 3% of its total metabolism when swimming at basal speeds.

Within the gills, O_2 is extracted from and CO_2 delivered to the water. Here, as in other structures dealing with energy transfer in the tuna, there exist modifications for rapid exchange. Within the secondary lamellae of the gills, blood flows obliquely to the long axis rather than with it as in other teleosts (Muir and Brown 1971). This oblique pathway allows a greatly shortened length of the absorbing vessel, reducing the total blood pressure drop across the skipjack tuna's gill by 16 times. The short path length allows for small diameter absorbing vessels as well as thinner, more efficient lamellae. The latter reduces resistance to water flow. Large gill areas result from the increase in total number of lamellae and their length. These adaptations result in a gill, which, while delicately constructed and fine grained, has an area of from 4 to 30 times larger than other teleosts.

Thus with this large gill surface area, the tuna gill's effectiveness in removing oxygen from the water is higher than other teleosts'. Stevens (1972) has estimated that skipjack tuna can extract up to 90% of the oxygen in the water that enters the mouth. Other fish can extract from 10 to 30%.

Four techniques have been employed to estimate oxygen uptake: 1) Whole animal, in which one or more tuna are confined within a sealed tank and the drop in dissolved oxygen is measured as the tunas respire; 2) starvation experiments, where energy consumption is measured by loss of weight and caloric density; 3) in vitro experiments that measure oxygen uptake of various tissue samples; and 4) restrained experiments, where oxygen consumption is measured from a perfused, paralyzed fish.

Of these four techniques, the measurements of oxygen consumption from fish swimming in enclosed chambers is the most common. Gooding et al. (1981) found that skipjack tuna's "standard" metabolic rate (SMR) was two to five times that of similar-sized, active non-tuna species. However, the true SMR for tunas is oxygen consumption rate at zero activity. This true rate must be extrapolated from rates collected from fish swimming at various voluntary speeds. The regression relating consumption rate to size and swim speed is as follows:

$$\log VO_2 = -1.20 + 0.19 \log W + 0.21\ S$$

where VO_2 = oxygen uptake (mg O_2/g per h)
W = fish weight (g)
S = swim speed (body lengths/s).

Of note is the weight exponent of near 0.2 compared with −0.2 of typical fish. Because the swim speed of routinely active skipjack tuna is inversely related to weight, routine metabolic rate is virtually independent of fish weight.

Lacking any caloric input, skipjack tuna lose mass and caloric density from their tissues from metabolic demand. The oxycalorific equivalent relates oxygen uptake values to those of calories transferred, 3.4 cal/mg O_2. A tuna swimming at its weight-dependent characteristic swimming speed (about 1.4 body lengths/s) has an energy demand (from Gooding et al. 1981) of $\log VO_2 = -0.54 + 0.08 \log W$. Thus, a 1,500 g skipjack tuna, swimming at its characteristic respirometer tank speed would consume 64 kcal/d. In a fasting fish, the energy comes from mobilization of body tissues; Kitchell et al. (1978), citing other sources, estimated that 20% overhead must be obtained from the tissues; the overhead pays for the deamination of proteins (15%) and the excretion of nitrogenous waste (5%). This will add an additional requirement of 16 kcal/d: $80 - (80 \times 0.2) = 64$.

The energy content for a whole skipjack tuna is approximately 1.46 kcal/g, which for our 1,500 g example is 2,190 kcal. Thus, a skipjack tuna swimming at 1.4 body lengths/s should lose about 3.7% of its total energy per day.

How does this compare with a real, fasting fish? Work at the Kewalo Research Facility demonstrated that starving skipjack tuna lose weight at 1.8%/d. But weight loss is not the complete story. Fish utilize fat and hydrate as they starve, so weight loss underestimates energy loss (Kitchell et al. 1977). They estimate that skipjack tuna lose about 1.8% of energy content per unit weight per day. This change of caloric density is added to the absolute weight change to yield an independent estimate of energy loss of 3.6%, which compares favorably with the 3.7% figure estimated from respiration measurements.

Gordon (1968) estimated metabolism from still another approach. Metabolic rates of unstimulated, minced muscle from skipjack and bigeye tunas were measured. Both red and white muscle preparations were employed. Values for red muscles averaged 2 mg O_2/g per h, for white muscle, 0.4 mg O_2/g per h. Tuna muscle is obviously a fast respiring muscle comparable with rat thigh muscle at its physiological temperature (Gordon 1968). Another interesting aspect of this work is the lack of much of a temperature effect upon respiration; a Q_{10} of virtually 1 is observed. Dizon et al. (1977) also observed this temperature compensation of swimming speeds. Perhaps this rapid temperature compensation, something observed in other animals whose habitats have rapid temperature changes, is an adaptation for their behavior of fast, continuous, vertical movements from the thermocline to the surface.

One difficulty in determining respiration of tunas is to arrive at a common level of activity which produces a respiration rate which can be compared with other fish. Usually this value is the SMR, which is defined as the energy requirements of a postabsorptive animal completely at rest. Tunas cannot stop swimming so this activity level is meaningless. Gooding et al. (1981) referred to the routine respiration rate, that is, the energy requirement of a tuna swimming at its "characteristic" speed. A standard rate can be determined from the routine measurement by extrapolating the swimming speed to respiration rate relation back to zero activity. Another approach is a direct measurement of respiration on a paralyzed, restrained fish (Brill 1979).

The SMR of 33 restrained fish ranging in size from 0.3 to 4.7 kg was:

$$\log VO_2 = 0.8987 - 0.437 \log W$$

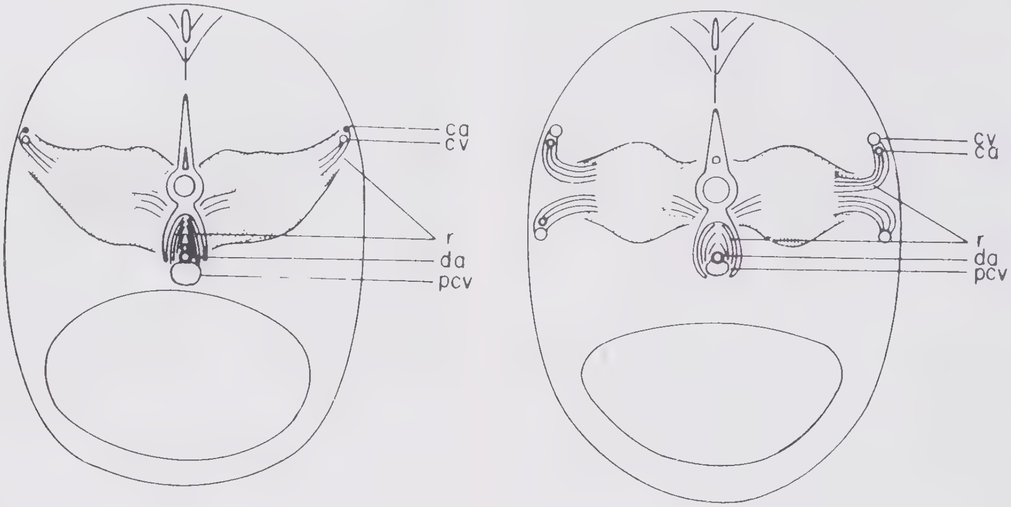
where VO_2 = SMR (mg O_2/g per h)
W = fish weight (g).

How do these values compare for other fish and for other methods of determining tuna respiration? Again the weight exponent is different. Other teleosts range from 0 to about −0.350 (quoted in Brill 1979). The value of −0.437 indicates that as body size increases, the SMR decreases relatively faster than for other teleosts which contradicts Gooding et al. (1981). However, the values predicted for the SMR by Brill's method compares favorably with the extrapolations of speed to zero of Gooding et al.'s regression. Compare 0.253 mg O_2/g per h determined by extrapolation of the regression to 0 and 0.324 mg O_2/g per h determined by Brill (1979). Brill reported that SMR's for tunas by either method exceed those reported for other teleosts by 5 to 10 times.

A logical next step is to inquire if high respiration rates correspond to a sensitivity to low dissolved oxygen (DO) levels in the habitat. Work reported in Dizon (1977) and Gooding et al. (1981) indicate that this is so. Skipjack tuna show definite signs of stress when DO levels fall below 3.5 mg O_2/l. Both investigations report dramatic increases in swim speed around 4.0 mg O_2/l. Dizon (1977) failed to observe any increased swim speed responses in yellowfin tuna at oxygen levels as low as 2.5 mg O_2/l. The swim speed response seems to be an adaptation to remove the animal from stressful habitats. An alternate explanation, increased ram jet ventilation, is not indicated since metabolic O_2 demands rise faster than the O_2 delivery to the gills as swim speed increases. Although these data indicate a great sensitivity to low O_2 environments, skipjack tuna can probably be conditioned to penetrate waters below 2 mg O_2/l for a reward, as was done with kawakawa (Chang and Dizon[14]). Hence the correlation of purse seining success with a shallow, O_2-deficient thermocline (Green 1967) is probably contradicted by the tunas' willingness to penetrate toxic habitats for short periods.

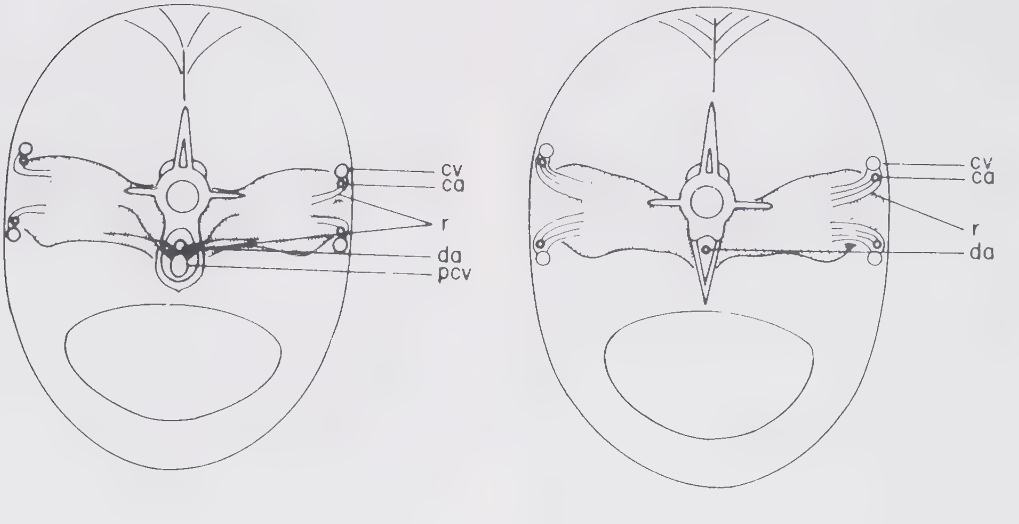
(3) Locomotion

For many years, the biochemistry of the skipjack tunas' unique intermediary metabolism has been researched by P. Hochachka and his students. The following is from Hochachka et al.'s (1978) excellent summary of the skipjack tunas' unique "power plant and furnace." Skipjack tuna, as other tunas, have an unusually large and distinct red muscle mass (8%) (Magnuson 1973), which is distinct and separable from the white (Fig. 53). This fact makes the tuna an excellent



E. lineatus

K. pelamis



T. albacares

T. thynnus

Figure 53. – Transverse sections of four tuna species showing the positions of the red muscle (shaded areas), the central and lateral rete mirabile (r). and the major blood vessels supplying the retia; dorsal aorta (da), posterior cardinal vein (pvc), cutaneous arteries (ca), and veins (cv). Note that the position of cutaneous arteries and veins in *Euthynnus lineatus* is reversed compared with that in other species and that only an epaxial pair is present. Also, *Thunnus thynnus* does not have a posterior cardinal vein (from Graham 1975).

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[14] Chang, R. K. C., and A. E. Dizon. Low oxygen levels (and temperature) as a barrier to voluntary movement of tunas. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

subject for muscle biochemistry studies. Previous data on teleosts supported separation of function for the two types of muscle: red is aerobic and is thus used for basal level swimming; white is anaerobic and is used for high speed and burst swimming. Recent workers suggest that there might be more overlap of function than heretofore suspected (sources cited in Hochachka et al. 1978 and in Brill and Dizon 1979). In general, the red muscle is highly vascularized and contains significant amounts of fat and glycogen, high amounts of enzymes of aerobic metabolism, and tremendous numbers of mitochondria. Red muscle thus appears totally aerobic, burning either carbohydrate, fat, or both. This is the typical teleost pattern. White muscle is, however, unusual. It contains high amounts of glycogen and concomitantly high glycolytic enzyme activities. But the enzymes for aerobic metabolism also occur in large quantities. Mitochondria exist in far greater numbers than in typical teleost white muscle, and fat droplets also occur. While white muscle contributes to burst swimming, supported by the "most intense anaerobic glycolysis thus far known in nature" (Hochachka et al. 1978: 154), most white muscle functioning is aerobic-based. This fact will be important when we later discuss thermoregulation.

The biochemical and physiological adaptations of the skipjack tuna characterize a high performance animal. This is obvious to anyone familiar with the morphology of the tunas. Strong selection pressures have operated to create body and fin configurations, swimming movements, and musculature to minimize drag and maximize thrust production per unit of input energy. Adaptations for reducing drag are more extensive in the tunas than perhaps in any other group. The skipjack tuna has an almost perfect body shape for longitudinal streamlining (Magnuson 1978). Drag reaches a minimum when maximum body thickness is 22% of length (Webb 1975). In contrast, the wahoo has a ratio of 12% (Magnuson 1973).

Turbulence is reduced by the presence of longitudinal, horizontal keels on the caudal peduncle (Webb 1975; Magnuson 1978). Similarly, the midline finlets across the dorsal and ventral portions of the posterior quarter of the body direct the water in a smooth flow as the tail beats in rapid, but low amplitude oscillations. The avoidance of turbulent flow around the fish results in lower drag. The oval peduncle, faired with the lateral bony keels, slips back and forth through the water with a minimum of resistance and yet provides a strong link with the high aspect, lunate tail. Drag producing structures are absent or reduced or can be removed from the water stream. No scales are present, save at the corselet, so the body is smooth. The eyes, nares, and mouth structures are almost perfectly faired into the body surface. The dorsal and pelvic fins are used only during turns so in straight-line swimming, the dorsal fin is slotted into the back and the pelvics are appressed into grooves. The pectoral fins provide lift to the negatively buoyant body and must remain in the water stream. However, when the skipjack tuna turns, the outer fin is appressed into a lateral groove on the body surface and its body pivots. Magnuson (1978) stated that during burst swimming, both pectoral fins are appressed into their respective body depressions, thus presenting a smooth body surface. Tuna fins have high aspect ratios; the length is long with respect to the width. Induced drag is relatively smaller for this fin shape (Magnuson 1978).

Yuen (1966) has recorded swimming speeds from skipjack tuna using cine techniques from a ship's observation chambers at sea. Speeds ranged from 0.5 to 14.4 body lengths/s. Dizon et al. (1978), employing ultrasonic tracking methods, recorded swimming speeds that clustered around 2 body lengths/s—not exceptionally fast, but they observed that sometimes the tuna would maintain speeds above 6 body lengths/s for over 30 min, and over 3 body lengths/s for over 240 min. Trout, in contrast, can only maintain 5 body lengths/s for < 5 min (Brett 1973). But we doubt that tunas are the fastest fish; Fierstine and Walters (1968) compared acceleration times of wahoo and yellowfin tuna and found that wahoo could accelerate around six times faster. While this is not surprising in a "lurking" predator like the wahoo, it provides insight into tuna design criteria. The impression that emerges is that the skipjack tuna should be viewed as a sustained performer, continually swimming at speeds considerably above most other teleosts', but perhaps not capable of the high speed bursts of the lurking predators.

Small tuna species (at least as adults) are totally lacking in a swim bladder and are, as a result, negatively buoyant (Magnuson 1973). Perhaps this is an adaptation to allow them to rapidly forage throughout the water column without danger of embolism. The ultrasonic studies reported by Dizon et al. (1978) showed continuous vertical movement that ranged between the surface and 273 m; these were sometimes completed in less than a minute.

Because the fish are negatively buoyant, lift must be provided to maintain hydrostatic equilibrium. The pectoral fins provide most of this lift (Magnuson 1973). Since lift is generated from the forward motion of the fish, the necessity of maintaining hydrostatic equilibrium imposes a minimum swim speed on the skipjack tuna. If speeds fall below this minimum, insufficient lift is generated and the fish either sinks or must resort to tail-down-head-up swimming behavior or a kind of flapping of the pectoral fins. The minimum swimming speed of skipjack tuna (Fig. 54) falls as size increases, from above 3 body lengths/s for a 12 cm animal to below 1.5 for a 100 cm one (Magnuson 1973). Incidentally, Magnuson (1973) reported that the minimum speeds predicted for skipjack tuna are identical to those predicted by Shuleikin (cited in Magnuson 1973) as most efficient for migration by aquatic species.

Measurements of drag by the various body and fin components can be used to estimate power consumption. Magnuson (1978) and Magnuson and Weininger (1978) provided accurate estimates of body dimensions and drag estimates for the various tunas. Dizon and Brill (1979) and Gooding et al. (1981) have used these to determine power required and heat generated at various swim speeds. An estimate for the 1,500 g example skipjack tuna's theoretical power uptake can be calculated by the following.

1) Total input power to swim is the sum of the power required for caudal thrust divided by the muscle efficiency of the propulsion system (20%) (Webb 1975) and added to the power required for nonswimming processes (Brill 1979; SMR, see Section 3.61(2)).

2) Thrust power must be equal to drag force multiplied by velocity (power equals force times velocity) and is estimated by:

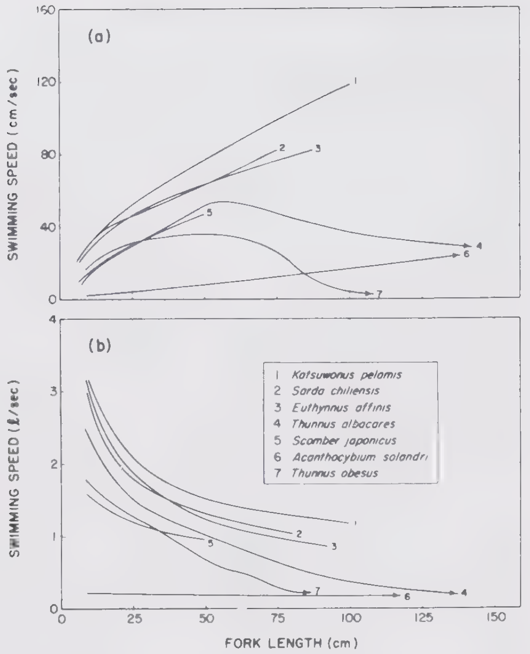

Figure 54.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec (from Magnuson 1978).

$$P = (0.5 \times \varrho \times S \times V^2 \times \mathrm{Cd} \times 10^{-7}) \times V \times 253$$

where P = required thrust power (mg O_2/h)
ϱ = water density (1.0234)
S = surface area (0.4 L^2, where L = fork length)
V = velocity (centimeters/s)
Cd = coefficient of drag (dimensionless number relating surface area and velocity to drag force)
253 = a multiplier that converts watts to mg O_2/h, assuming an oxycalorific equivalent of 3.4 cal/mg O_2.

3) The coefficients of drag and body surface area have been calculated for skipjack tuna and others by Magnuson and Weininger (1978). For the purposes of this treatment, a simple 0.4 L^2 assumption is sufficient for body surface and an estimate of drag coefficient of:

$$\mathrm{Cd} = 10\left(\frac{\varrho L V}{\mu}\right)^{\text{[illegible]}}$$

where μ = water viscosity (0.0096).

The 1,500 g (43 cm) example skipjack tuna swimming at 1.4 body lengths/s should theoretically have a coefficient of drag of about 0.02, require 0.028 mg O_2/g per h of thrust and thus five times as much input power to the propulsion system to "pay" for the 20% efficiency of the system (80% is lost as heat, some of which warms the body). Input required is thus 0.14 mg O_2/g per h, which must be added to the power required for nonswimming functions such as osmoregulation. Using Brill's (1979) SMR relationship (0.35), the total required power should be 0.49 mg O_2/g per h, which compare well with Gooding et al.'s (1981) measured value of 0.498 mg O_2/g per h.

3.62 Thermoregulation

Stevens and Neill (1978) characterize the life history strategy of the tunas as energy speculators. Tunas gamble relatively large amounts of energy to quickly move through their forage-poor environment and anticipate correspondingly large energy returns. Adaptations for energy speculation have produced many of the unique specializations that we have so far described for fast swimming and rapid energy overturn. It has also presumably brought them to the verge of homeothermy. Tunas, and some pelagic sharks, maintain their body temperature above that of the surrounding water. As indicated in earlier sections, tunas, particularly skipjack tuna, have exceptionally high metabolic rates. Because the propulsion system is only 20% efficient, 80% of the input power to the system is available to heat the tissues. In most teleosts this excess heat is carried from the trunk muscles by the venous system to the gills, where the heat is lost to the water. Thermal equilibrium occurs at a much faster rate than the mass transport of O_2 and CO_2, so the heated venous blood thermally equilibrates with the seawater. As a result, excess temperatures of most teleosts never exceed a few tenths of a degree.

The thermoconserving mechanism taxonomically distinguishes the 13 species of true tunas from the rest of the scombrid family (Klawe 1977; Collette 1978). Heat is transferred from the venous to the arterial sides of the circulatory system in a system of countercurrent parallel arterioles and venules in close contact (Fig. 53). These are the rete mirabile ("wonderful nets"). Tunas have four different types:

1) Cutaneous retia served by cutaneous arteries and veins which are unique among teleosts. This system is very large in bluefin tuna and provides all of the muscle blood flow. In the skipjack tuna, however, it is small and of presumably minor importance (Stevens and Neill 1978).

2) Visceral retia are found within the bluefin tuna, albacore, and bigeye tuna but are absent in the skipjack tuna.

3) Eye and brain retia are found in the bluefin tuna and albacore but unknown in the skipjack tuna, although they exhibit elevated brain temperatures.

4) Central rete are well developed in the skipjack tuna and other small tunas. It is located directly beneath the vertebral column. Stevens et al. (1974) has described the retia in great detail (Fig. 55).

Because of the countercurrent rete, metabolic heat is trapped within the muscle mass of the body with excess temperatures ranging from 1° to 21° above the surrounding water (Barrett and Hester 1964; Carey et al. 1971; Stevens and Fry 1971; Graham 1975; Dizon et al. 1978; Stevens and Neill 1978).

Tunas have several thermoregulatory options (Dizon and Brill 1979):

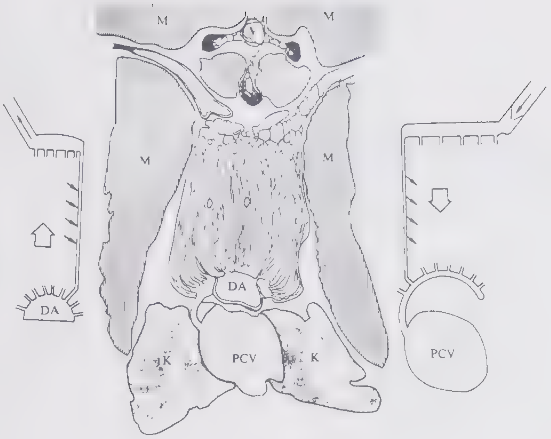

Figure 55.—Schematic drawing illustrating the major features of the vascular heat exchanger of skipjack tuna. DA, dorsal aorta; K, kidney; M, muscle; PCV, post-cardinal vein; V, vertebra. Left inset shows pattern of arterial blood flow; right inset shows patterns of venous blood flow; small arrows indicate heat transfer from venules to arterioles in the exchanger (from Stevens et al. 1974).

1) Behavorial thermoregulation

Since tunas are mobile and live in a heterothermal environment, they can behaviorally select optimal thermal habitats. Except for bluefin tuna, the distribution of the others is narrowly circumscribed by temperature (Sund et al. 1981). And because they "store" heat, they can behaviorally regulate activity to alter heat production: less activity means less heat produced.

2) Passive thermoregulation

Any process that stabilizes body temperature without requiring nervous system intervention can be characterized as passive thermoregulation.

Water temperature- and swim velocity-related heat production have been suggested as affecting body temperature. Water temperature affects water viscosity and density and thus influences drag forces which, in turn, alter the energetic requirements of swimming.

Thermal inertia might explain much of what was considered physiological thermoregulation in the past (Carey et al. 1971; Neill and Stevens 1974; Neill et al. 1976; Dizon and Brill 1979). Because of the retia, heat is exchanged with the environment at a much more reduced rate in tunas than in similar-sized teleosts; body temperature changes in tunas thus can significantly lag behind environmental changes.

As swim velocity increases, the surface heat dissipation rate is increased. However, it does not appear that this process is sufficient for stabilizing body temperatures in response to increased heat production as tuna swim faster (Dizon and Brill 1979).

3) Physiological thermoregulation

Activity-independent thermoregulation requires that the nervous system has the ability to recognize thermoregulatory needs and alter the effectiveness of thermoconserving structures.

It is difficult to use field data as evidence for physiological thermoregulation. Barrett and Hester (1964) determined a regression between sea surface temperature (Ta) and body temperature (Tb): $Tb = 0.58\ Ta + 16.39$. Presumably, if Tb was constant over a great range of Ta's, one could assume a thermoregulatory ability. In skipjack tuna, the slope is different from unity implying some thermoregulatory process. However, other workers (Carey and Teal 1969; Stevens and Fry 1971) observed muscle temperatures quite different from Barrett and Hester's (1964), although the fish were taken in waters of the same temperature. Still, Stevens and Fry (1971) concluded that skipjack tuna could maintain a fixed Tb in waters ranging from 25° to 34°C; that is, that they do regulate. Conclusions drawn from such field evidence, however, are not justified because the thermal histories of the fish prior to capture were unknown. Very cool water is available to the fish within less than a minute before the time it is caught, boated, and measured. Consequently, sea-surface temperature does not necessarily represent the real habitat temperature. Moreover, thermal inertia causes Tb to lag behind apparent changes in Ta, and activity of the fish is a critical determinant of heat production and presumably Tb. All these affect the thermal history of the fish before they are captured.

To differentiate between thermoregulatory options, experiments must be conducted that measure Tb and activity at specified, constant Ta's. Dizon et al. (1978) and Dizon and Brill (1979) investigated thermoregulatory performance in skipjack and yellowfin tunas, where Ta could be fixed and Tb measured by ultrasonic telemetry. Swim speed in an annular tank was constantly monitored with photocells. Under these conditions a simple Tb versus Ta regression reveals little temperature adjustment. Body temperature is clearly dependent upon Ta: $Tb = 3.14 + 0.97\ Ta$. Dizon et al. (1978) estimated heat production (H_p) using the same techniques outlined in the previous section for determining total power input. Heat production is the input power, minus the output power dissipated as thrust, plus the SMR. Use of these relationships allows comparisons to be made between fish of different sizes swimming at different speeds. An index of whole-body thermal conductance can be developed,

$$H_L = k\,(Tb - Ta)$$

where H_L = steady state heat loss.

Since the fish is assumed to be in steady state, that is, Tb is constant, then H_L must equal H_p. In contrast to yellowfin tuna, skipjack tuna were found to exhibit a great deal of variability in the whole-body thermal conductance over the temperature range from 20° to 30°C. (If regulation were occurring, increases in Ta should be accompanied by increases in H_L so that Tx would get smaller where $Tx = Tb - Ta$.) Nevertheless, even though H_p is tightly linked to swim speed, changes in swim speed were not accompanied by changes in body temperature. Clearly, some mechanism existed in skipjack tuna to alter either the pattern of H_p, heat loss, or both.

Dizon and Brill (1979) extended the above experiment by forcing tunas to swim at high speeds in water temperatures approaching their upper lethal limit. Under these conditions, if physiological regulation was possible, the tuna would demonstrate it. Swim speed was increased by force feeding plastic-coated weights to 23 fish. Only three survived the treatment long enough to collect data. Two of the fish were able to significantly increase whole-body thermal conductance and one with no decrease in swim speed. Dizon and Brill (1979) consider this true physiological thermoregulation.

There are two situations in tunas which require some thermoregulatory adjustments: 1) *Tx* should be increased or decreased when ambient temperatures approach lethal limits, and 2) extremely rapid increases in heat production accompanying increases in swim speed must be dissipated to prevent muscle overheating. The tuna could meet these two exigencies with 1) some physiological process that would alter the effectiveness of the heat exchanger, and 2) changes in the relative contribution of the red and white muscle fibers to swimming.

Prevention of overheating presents no problem. There has been much in the literature on the overheating of large, active tunas in warm water, notably Barkley et al. (1978) and Sharp (1978), to define inhabitable regions in the ocean. However, there is no physiological data indicating that tunas can overheat under free-swimming normal conditions. If the notion that the white muscles are only used for high speed swimming is discarded, a way out of the overheating conundrum is apparent. In the section on energetics, the argument was made that white muscle fibers are graded into contributing to swimming propulsion at a relatively low swim speed (Hochachka et al. 1978; Brill and Dizon 1979). White muscle fibers are vascularized by pathways which bypass the vascular heat exchanger (Kishinouye 1923; Godsil and Byers 1944) so the heat or a portion of it is lost at the gills, like other nonthermoconserving fish.

Control of the relative contribution of the two fiber types to swimming might also serve to adjust *Tb* in response to the first exigency. At high environmental temperatures, the tuna might rely more on the white muscles, which add to the body heat burden to a lesser extent than the red. In addition, there might well be some regulation of the effectiveness of the heat exchanger itself.

In summary, tunas have relatively large numbers of processes to deal with thermal challenges. They obviously can employ behavioral responses of seeking new habitat or reducing or increasing swim speed. Thermal inertia helps stabilize body temperatures during periods of rapidly changing environmental temperatures. Physiological mechanisms exist as seen in the observation that heat production and body temperature are not always linked.

As to the question, "Why be warm in the first place?' many ideas have been suggested, but no real answers have emerged. Because of the fast swimming, energy speculative nature of the tuna, most suggestions have centered on swimming. The original assumption (Carey et al. 1971) is that higher temperatures increase muscle power. However, Walters and Fierstine (1964) found that a yellowfin tuna, whose body temperature was twice that of a wahoo, exhibited speeds only slightly greater and acceleration times considerably less. Neill and Stevens (1974) suggested that recovery time from anaerobic activity might be lessened because of the increased temperature. Perhaps energetic efficiency is enhanced, or there are biochemical advantages to the thermoconserving structures. Hochachka et al. (1978) felt that the tuna has greater control over its highly charged metabolsim. Given a Q_{10} of 2, a twentyfold change in metabolic rate can be converted to a fortyfold change, if the change is accompanied by a 10° rise in temperature. Perhaps the retia temperature function is only secondary; its main one may be to retard mass transfer of lactic acid, the byproduct of anaerobic glycolysis. Then lactate from the white muscle would pass to the red muscle, where it would be metabolized by that tissue's liverlike enzymes (Stevens and Neill 1978). But much of the white muscle circulation bypasses the rete mirabile entirely.

There also might be benefits occurring simply from stability of the body temperature. Neill and Stevens (1974) and Neill et al. (1976) suggested also that because of the thermal inertia, perception of very weak horizontal gradients could be accomplished. But because of the skipjack tuna's habit of constantly making vertical migrations (Dizon et al. 1978), we wonder if the horizontal gradients have much meaning to the tuna.

3.63 Hypothetical habitat of skipjack tuna

Barkley (1969) has hypothesized that the habitat of the adult skipjack tuna coincides with the area where a shallow salinity maximum occurs seasonally or permanently, whereas that of larval skipjack tuna coincides with the area having a permanent shallow salinity maximum. Thus, a hypothesized maximum depth and distribution can be mapped (Fig. 56).

Temperature and oxygen data can also be utilized to delimit distributions based upon size (Figs. 57-59). Barkley et al. (1978), based upon information from Neill et al. (1976), considered three environmental conditions that would be likely to operate to determine distribution of skipjack tuna. These are: 1) A lower temperature limit around 18°C, 2) a lower dissolved O_2 level around 3.5 p/m, and 3) a speculative upper temperature limit, ranging from 33°C for the smallest skipjack tuna caught in the fishery to 20°C or less for the largest.

According to the analysis, skipjack tuna larger than 11 kg should find relatively few habitable regions within the eastern tropical Pacific Ocean (Fig. 60). While this agrees with fishery data, the third condition does not seem to hold (see Section 3.62). The authors arrived at this condition by extrapolating from data obtained from restrained fish and by predicting temperatures for a fish swimming with red muscle only. These conditions could then result in thermal runaway; that is, a positive feedback system could be generated with muscle temperature increases causing faster swimming, causing increasing muscle temperatures. But as indicated in the previous section, tunas do not overheat even though they are very active in warm water. Some process intercedes to reduce temperature excess (Dizon and Brill 1979).

3.64 Responses to stimuli

(1) Vision

Nakamura (1968) studied the visual acuity of skipjack tuna and kawakawa using conditioning techniques. Tunas were taught to respond to targets bearing either vertical or horizontal stripes in order to receive food and avoid electric shock. At lower light levels, visual acuity of the two species was similar but at higher levels, the skipjack tuna did better (Fig. 61).

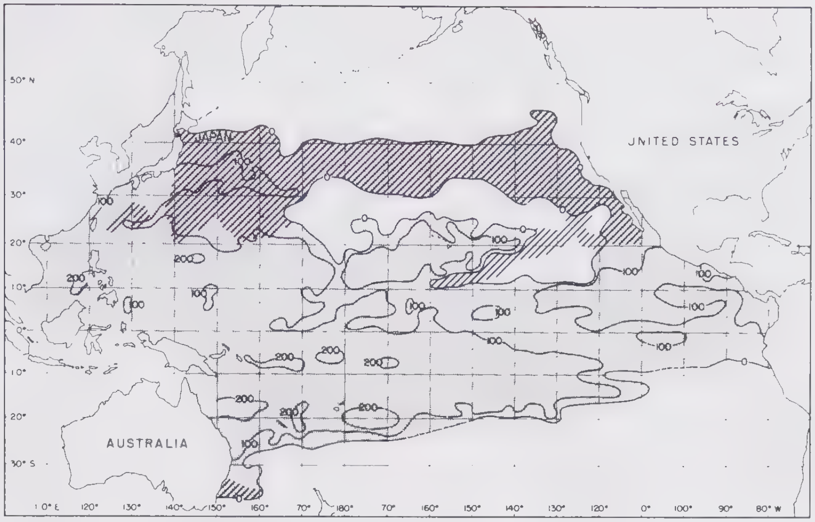

Figure 56.—Depth in meters of the shallow salinity maximum in the Pacific Ocean, based on all available oceanographic station data, averaged within areas of 2° of longitude by 2° of latitude. Regions where a shallow maximum is present during one or more quarters but not all year are indicated by hatching. A region analogous to the hatched area in the North Pacific must also be present in the South Pacific but cannot be shown due to sparsity of data (from Barkley 1969).

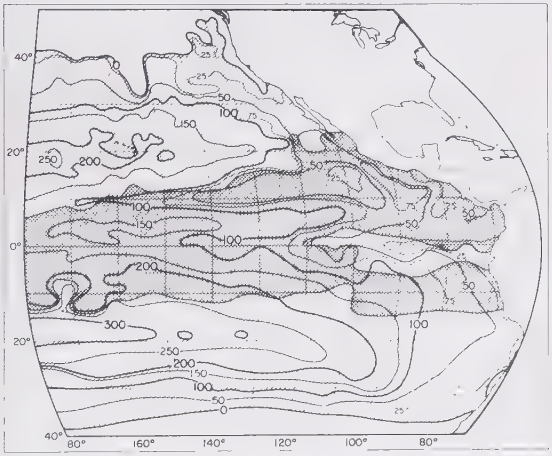

Figure 57.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml/l (5 p/m) isopleth of dissolved oxygen (crosshatched area). Contour interval is 50 m except for a few areas near the coast, where a 25 m contour interval is used (from Barkley et al. 1978).

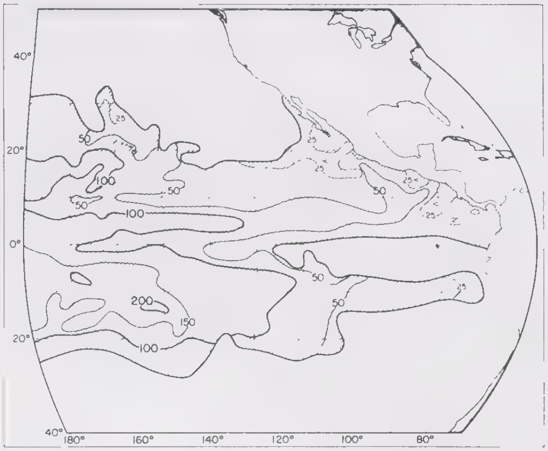

Figure 58.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of the 180° meridian, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24°C. Contours show the depth, in meters, of the 24°C isotherm (from Barkley et al. 1978).

The role of visual acuity in the life of pelagic fishes may involve, in addition to the detection of prey and predators, the recognition of transient body marks, such as the vertical bars exhibited by the skipjack tuna during feeding (Strasburg and Marr 1961; Nakamura 1962; Nakamura and Magnuson 1965) or during courtship (Iversen et al. 1970), as well as other permanent body markings. Nakamura (1968) calculated the distances of resolution of prey or body marks as 36 m, if the skipjack tuna were in waters having the same visibility conditions as that in the experimental tank. He also determined that the skipjack tuna could prey on objects as small as 0.9 mm, based on the minimum size of food particle that could be retained by the gill rakers, and that it would be able to resolve prey of this size at a maximum distance of 54 cm. The transient vertical bars on the flanks of skipjack tuna, being about 2 cm wide, would be resolved at a maximum distance of 12.4 m, whereas the permanent black longitudinal stripes on the belly, being 0.5 cm wide, would be re-

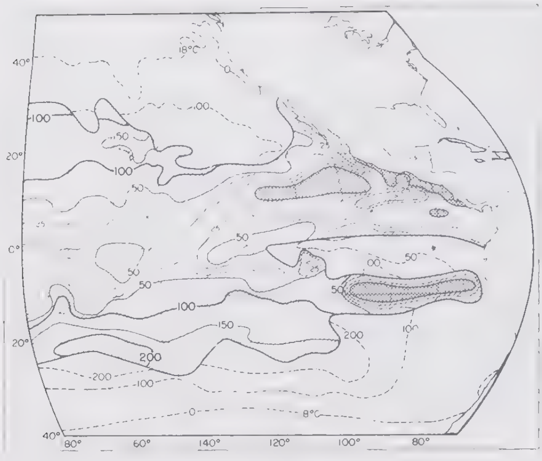

Figure 59.—Thickness of the hypothetical habitat layer (meters), for 6.5 kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Fig. 57) from the lower one (Fig. 56). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area, the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna (from Barkley et al. 1978).

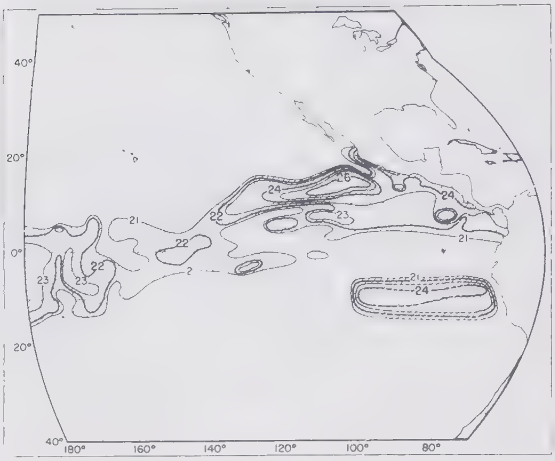

Figure 60.—Water temperature at those depths where the concentration of dissolved oxygen is 3.5 ml/l. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. Skipjack tuna weighing more than 11 kg require well-oxygenated water cooler than 21°C; they should find all the shaded areas stressful. Similarly, 4 kg skipjack tuna should find the area enclosed by the 26°C contour either too warm or too poor in dissolved oxygen. Smaller skipjack tuna would seldom encounter thermal stress in the eastern tropical Pacific, and can inhabit all areas by staying in the shallower, oxygen-rich layers (from Barkley et al. 1978).

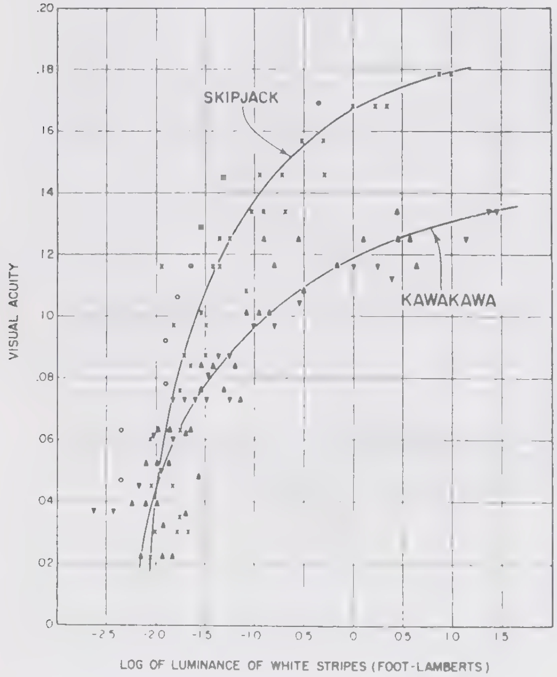

Figure 61.—Visual acuity curves of skipjack tuna and kawakawa, *Euthynnus affinis*, at adaptive illumination of 170 luxes (from Nakamura 1968).

solved at maximum distances of 3.1 m, again in waters having the same visibility conditions as those in the experimental tank. These conditions would be met in pelagic waters typical of the tropical ocean with an unobstructed sun at an altitude of 65°.

The presence of color vision improves perception, but tunas are color blind. Work by Tamura et al. (1972) and Kawamura et al. (1981) failed to find chromaticity-type S-potentials. This is a technique where electrical potentials are measured from the isolated or in situ retina. The chromaticity S-potential is considered by visual physiologists as a definitive test for color vision. The latter authors looked for but failed to find these potentials in yellowfin tuna; bigeye tuna; albacore; striped marlin, *Tetrapturus audax*; blue marlin, *Makaira nigricans*; and black marlin, *M. indica*. Tamura et al. (1972) recorded S-potentials from skipjack tuna, kawakawa, and frigate tuna and failed to find the chromaticity type. That these fish are color blind is consistent with the findings by Tester (1959) that tunas exhibited no color preference in behavior tests. Also, most wavelengths of light are rapidly attenuated with depth, so that the principal habitat of the pelagic fish is a monochromatic one. Munz and McFarland (1977) found only a single visual pigment in retinal extracts of wahoo, yellowfin tuna, kawakawa, black marlin, and blue marlin. This is also a strong indicator of the lack of color vision.

(2) Temperature

Skipjack tuna have thermal receptors and can make behavioral decisions based on temperature stimuli. Dizon et al.

(1974, 1976), using heart-rate conditioning techniques, demonstrated temperature perception in skipjack tuna. Steffel et al. (1976) demonstrated that free-swimming, captive kawakawa could discriminate temperature thresholds of 0.10° to 0.15°C. We suspect that skipjack tuna can do as well because this degree of sensitivity has been demonstrated in other teleost species. Even though this seems like a high degree of sensitivity, horizontal gradients in the ocean are never likely to exceed 0.0001° to 0.001°C/m. This fact, and the tunas' habit of making continuous vertical movements through gradients of several degrees, makes it unlikely that they use the weak horizontal temperature changes as orienting cues.

(3) Mechanical

Sound does not seem to affect the behavior of skipjack tuna at sea (Strasburg and Yuen 1960). Noise produced by hammering on the hull failed to alter the behavior of the tuna being fished. However, it is doubtful that skipjack tuna are deaf. Iversen (1969) determined threshold curves (thresholds versus frequency) for kawakawa and yellowfin tuna. Thresholds were not remarkable when compared with other teleosts.

York (1974), on the other hand, found that sudden or irregular noise, as caused by worn bearings, a bent propeller shaft, a slack rudder, or changes in throttle with a "high revving" engine, caused schools of skipjack tuna as well as yellowfin tuna and albacore to sound. In addition, York reported some success in attracting skipjack tuna schools by playing back recordings of anchovies "breezing" and gannets diving.

(4) Chemical

Tests at sea to attract skipjack tuna using extracts from skipjack tuna, yellowfin tuna, and anchovy were either negative or inconclusive (Tester et al. 1954). Other substances, such as skipjack tuna blood sprayed in the water or skipjack tuna blood and body slime allowed to drain from the scuppers into the water failed to affect the behavior of the skipjack tuna (Strasburg and Yuen 1960).

4 POPULATION

4.1 Structure

4.11 Sex ratio

Most of the sex ratios reported in the literature are byproducts of studies on maturation and fecundity. No real use was made of the sex ratio information including attempts to relate changes in sex ratio with maturation, size of fish, spawning season, or changes of availability or migration associated with attainment of maturity. The discussion below will proceed by ocean and all ratios are presented as number of males to number of females.

For the Atlantic Ocean, Batts (1972c) presented data obtained from recreational catches off two locations in North Carolina, U.S.A., in 1964-66. Over all years and both areas, the sex ratio favored females in all but one case and ranged from 1.06:1 to 0.58:1, averaging 0.86:1. Cayre (1979) found a ratio of 0.95:1 for a small sample collected in Dakar from Senegalese purse seiners fishing in the Gulf of Guinea. Chur et al. (1980) likewise reported that the sex ratio of fish captured by purse seiners in the eastern tropical Atlantic from 1969 to 1977 did not differ from 1:1.

For the Indian Ocean, Raju (1964a) found males predominating in most months, especially for older age groups in samples collected in the Minicoy Islands. Marcille and Stequert (1976) and Stequert (1976) presented monthly data on the sex ratio of fish collected from Japanese bait boats fishing off the northwest coast of Madagascar from February 1974 to March 1975. There was no apparent trend in the monthly data and all but one of the values favored females. For the entire period, the sex ratio was 0.83:1 and ranged from 1.01:1 to 0.72:1.

For the Pacific Ocean, Schaefer and Orange (1956) found that more females (0.73:1) occurred in the samples from the young fish taken in the eastern tropical Pacific fishery; however, sex could not be determined for a large proportion of the samples. Yoshida (1960) reported that the sex ratio was 1.05:1 for samples collected in the central South Pacific. In Hawaii, Brock (1954) showed that males predominated in the catches during most time periods (1.16:1 overall) and differed significantly from 1:1 in the September-December period in 1949 and 1950 (1.64:1 and 1.32:1, respectively). Also, catches from experimental trolling in inshore Hawaiian waters (Tester and Nakamura 1957) showed a predominance of males (1.57:1). For the northern Marshall Islands area (Marr 1948), males again predominated (1.60:1). For fish taken off Taiwan, Hu and Yang (1972) reported a preponderance of males (1.31:1) in the 50-59 cm FL interval, while the ratio was 1:1 in the adjacent 10 cm FL intervals. Monthly data showed considerable variability, for example, from 3.01:1 to 0.64:1, but there was no apparent trend. Off Japan, the ratio was reported to be 1.09:1 (Waldron 1963). Wade (1950) reported that females dominated in the Philippine catch with a ratio of 0.86:1. Likewise in New Zealand, females are reported to dominate the catch, with the ratio being 0.76:1 for fish caught by purse seine over the period December 1976-March 1978 (Habib 1978).

These statistics suggest that those fisheries known to depend on young, immature fish have sex ratios favoring females while those fisheries harvesting predominately older, spawning age fish exhibit sex ratios favoring males.

4.12 Age composition

Few tables of age composition have been presented in the literature because of the inherent difficulties in aging skipjack tuna as pointed out in a previous section. For the most part, age composition has been determined from tables of size composition using various growth equations. Until skipjack tuna can be aged with certainty and with greater ease than is currently possible using otoliths or other hard parts, little use is likely to be made of tables of age composition.

4.13 Size composition

Since all fisheries capture skipjack tuna over a restricted size (age) range and most over a limited geographical range, the size-frequency distributions and other measures of size composition given below are in all likelihood not representative of any complete stock or population. Length-frequency distributions have been published most commonly to simply describe the size composition of the catch and document seasonal changes in a fishery. They have been used less frequently to study recruitment, relationships among areas or fisheries, growth, and gear selectivity. From another perspective, Sharp (1976, 1978, 1979) and Barkley et al. (1978) proposed that the temperature and oxygen structure of the oceans in interaction with the physiological properties of skipjack tuna limits the distribution of larger individuals. This subject is discussed more fully in Section 3.63.

(1) Length composition

All length measurements are fork length unless otherwise stated. Modes were determined by visually inspecting the distributions in all but one case.

(a) Pacific Ocean

For the eastern tropical Pacific Ocean, Broadhead and Barrett (1964) presented quarterly length-frequency distributions for four northern areas of the fishery in 1954-60. While there was considerable variability among years, the distributions for 1956 (Fig. 62) show that the four areas generally had a single mode, though of different size. The Baja California area tended to have consistently smaller fish (40-50 cm), while the Gulf of California, the Mexican coast, and the Revillagigedo Islands tended to have more fish between 60 and 70 cm. Data presented for more recent periods, for example, 1967-79 for the entire Commission's Yellowfin Regulatory Area (IATTC 1980), likewise show considerable variability among years and, probably because several areas were combined, the distributions tended to show multiple modes. Diaz[15] showed that the length-frequency distribution from purse seine catches frequently shows more large fish than do those for bait boats. His data also indicated that fish off Ecuador were mostly between 50 and 60 cm. While the skipjack tuna taken in the northern area of the fishery are generally considered to comprise a single stock, the variability shown here as well as the morphometric and genetic findings of Sharp (footnote 4) suggest that a considerable amount of heterogeneity may exist.

For Hawaiian waters, Rothschild (1965) compared the third quarter length-frequency distributions for Baja California (taken from Broadhead and Barrett 1964) with those from Hawaii (Fig. 63) and found a remarkable similarity for the small modal group in 1954 and 1960. In 1959, however, the two distributions differed considerably. Rothschild (1965) inferred from this figure and other evidence that the small fish in the Hawaiian and eastern Pacific (at least Baja California) fisheries have a common origin and that the origin is in the central equatorial Pacific Ocean. However, from Figure 63 and other evidence, it is apparent that there are differences in size distributions between the eastern tropical Pacific and Hawaiian fisheries. The Hawaii size frequency is bimodal or trimodal, including small fish as in the east but large fish in addition. Summarizing over years for the winter months in the Hawaiian fishery, modal groups are found at approximately 35, 50, and 75 cm, while in the summer months they are found at approximately 45 and 70 cm. Whereas Brock (1954) found progression of modal groups and based a growth model on them, Rothschild (1965) found the progression to be irregular with instances of regression.

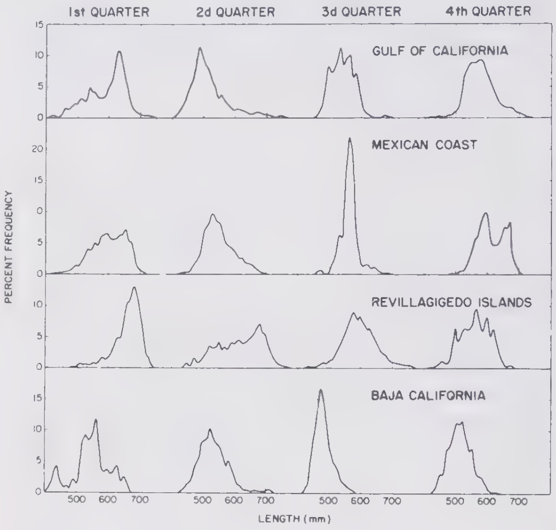

Figure 62.—Length distribution of skipjack tuna for 1956 by quarter of the year for the Gulf of California, Mexican waters, the Revillagigedo Islands, and coastal areas of Baja California (modified from Broadhead and Barrett 1964).

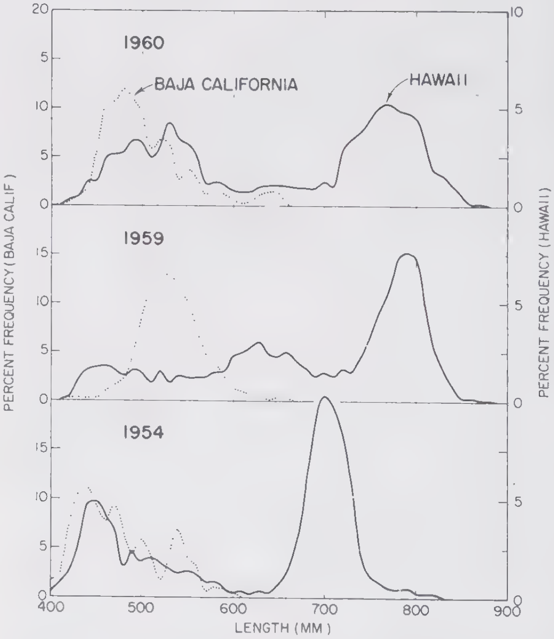

Figure 63.—Length-frequency distributions for skipjack tuna taken during the third quarter of the year from fisheries off Baja California and the Hawaiian Islands (from Rothschild 1965).

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[15] Diaz, E. L. 1966. Growth of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Internal Rep. 2, 18 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

For the equatorial region in the central Pacific Ocean, experimental longline catches showed the presence of fish from 47 to 84 cm (Shomura and Murphy 1955). While most of the fish were between 70 and 80 cm, longline catches are commonly believed to be biased toward larger individuals.

For the South Pacific, most data have resulted from exploratory fishing rather than from commercial or subsistence fisheries. Rothschild and Uchida (1968) found that experimental catches in the Marquesas Islands showed a trimodal distribution with modes at 47 (dominant), 67, and 75 cm. Bayliff and Hunt[16] presented data assembled from various sources for the Marquesas and Tuamotu Islands by various months from 1957 to 1959 and 1977 to 1980. In most cases, there were one or two size modes with the major one at approximately 50 cm and a lesser mode sometimes occurring around 70 cm. For the Society Islands, Bayliff and Hunt (footnote 16) again presented data assembled from various sources by various months from 1973 to 1978. Some of these data were collected from the subsistence fishery in Tahiti. There appeared to be three modes, which in many cases fell roughly in the 40-50, 60-70, and 80-90 cm intervals; the total range was 32-91 cm. They also found some evidence of progression of modes which they felt indicated growth, but Josse et al. (1979) concluded otherwise. Moving slightly to the east, a single mode was found at 45-50 cm for samples taken at Pitcairn and Gambier Islands in 1980. For American Samoa, Kearney and Hallier (1978c) presented data for May-June 1978 showing a range of 39-64 cm with modes at about 45 and 60 cm. The sizes of fish collected in West Samoa in July 1978 were somewhat smaller, 36-58 cm, and showed only one mode around 49 cm (Kearney and Hallier 1978b). Moving slightly westward into Tuvalu, the length frequency of fish collected in June-July 1978 had a range of 35-66 cm and exhibited three modes at around 38, 52, and 61 cm (Kearney, Hallier, and Kleiber 1978). Slightly to the north in the Gilbert Islands (Kiribati), the range of fish taken by exploratory bait boat in July 1978 was 38-62 cm, with modes around 40 and 47 cm (Kearney and Gillett 1978). In Fiji the FAO bait boat development project obtained fish ranging in size from 29 to 84 cm in 1972, 1973, 1974 (FAO 1974a). Two modes were apparent at approximately 46 and 54 cm. Length-frequency distributions from the developing purse seine fishery in New Zealand (Vooren 1976; Habib 1978; Habib et al. 1980a, b, c) indicated a size range of 30-70 cm, but generally there was only one strong mode at 45-50 cm with minor modes around 35 and 55-60 cm appearing in some month/area strata. At Norfolk Island, exploratory bait boat catches in March 1980 showed a size range of 42-68 cm and a mode at around 64 cm (Kearney and Hallier 1980a).

For the southwestern Pacific, Kearney and Gillett (1979) reported that off Queensland, Australia, the size range of fish taken by exploratory bait boats was 35-70 cm with modes at 48 and 62 cm; off New South Wales, the range was 39-66 cm with modes at 46, 51, and 60 cm. In New Caledonia, data from experimental trolling in 1956-60 showed a range of 40-75 cm standard length (SL) with a strong mode at 50 cm SL and possibly minor modes at 54, 60, 65, and 72 cm SL (Legand 1971); whereas exploratory bait boat catches in December 1977-January 1978 showed a range of 38-74 cm, with modes around 43, 50, and possibly 55 cm (Kearney and Hallier 1978a). In New Hebrides data from exploratory bait boat catches in December 1977-January 1978 indicated a size range of 41-78 cm with modes near 45 and 51 cm (Kearney Lewis, and Hallier 1978). In Papua New Guinea, exploratory bait boat catches showed a range of 36-66 cm with a mode at 56 cm (Kearney and Hallier 1979), whereas the size range for commercial bait boat catches was 46-69 cm (Wankowski 1980). For the Japanese purse seine fishery to the northeast of Papua New Guinea, Honma and Suzuki (1978) presented data showing catches ranging from 29-30 to 73-74 cm in 1970-74 with a single mode ranging from 44 to 53 cm. There was no indication of a progression of modes with time. For Indonesia, Simpson (1979) presented information on the size composition of the bait boat fishery in Ambon, Bitung, Sorong, and Ternate. In February 1977 and January-May 1978, the size range was 30-72 cm with a single mode at around 50 cm. A more ambitious sampling project is now being conducted by Indonesia (and Philippines) in cooperation with the U.N. South China Sea Fisheries Development and Coordinating Programme and a report on the first year's sampling (1979-80) will be available shortly.

For the northwestern Pacific, we will first discuss the Trust Territory of the Pacific Islands, then Philippines, Taiwan, and Japan. Within the Trust Territory for exploratory Japanese longline operations south of lat. 10°N in 1950-51, the size range was from 47 to 82 cm with a single mode at 57 cm (Murphy and Otsu 1954). For exploratory bait boat catches along a cruise track from the northern Mariana Islands through Truk and Ponape to Kosrae in November 1979, the size range was 27-60 cm with modes at 30 and 52 cm (Kearney and Hallier 1980b). For the northern Marshall Islands, experimental trolling catches had a size range of 34-74 cm with modes at 45, 55, and 65 cm (Marr 1948). The size composition of the catches made by the Japanese distant water bait boat fleet in an area encompassing the northern Mariana Islands and Palau Islands during June 1964-April 1966 showed a range of 35-75 cm (Kasahara and Tanaka 1968). The distributions were multimodal in most months with modes falling in the 40-50, 50-60, and 60-70 cm intervals. Progression of the smallest mode was quite apparent. Data collected during 1965 from the bait boat fishery based in Palau Islands indicated a range of 30-74 cm, and a prominent mode at 50 cm in June and 58 cm in October (Higgins 1966); whereas data collected in 1967 and 1968 showed evidence of at least two modes, one between 45 and 50 cm, and the other around 60 cm (Uchida 1970). Since 1964 the Tohoku RFRL, Japan, has been issuing reports on the Japanesse southern water fishery (Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory undated a, b, c, d), which was initially limited to the area within the Equator and lat. 24°N, and long. 125° and 150°E. Initially, the data were obtained only from bait boats; the season usually started in June and was over by April of the following year, and the area fished was from the northern Mariana Islands to Palau Islands. Now, purse seiners have entered the fishery and the fishing area has expanded to well below the Equator and east to long. 150°W. A few generalizations can be gleaned from these reports. First, it is apparent that catches from shoal-associated schools generally had a single mode around 45 cm, whereas open ocean catches were multimodal. Second, purse seine catches generally exhibited only two modes around 40 and 50 cm whereas bait boat catches exhibited several modes. Third, there were great variations in the frequency distributions among months, years, and areas as well as variations in the amount of fishing effort expended in these time/area strata that make interpretations difficult.

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[16] Bayliff, W. H., and G. A. Hunt. Undated. Exploratory fishing for tunas and tuna tagging in the Marquesas, Tuamotu, Society, Pitcairn, and Gambier Islands. Inter-Am. Trop. Tuna Comm., Spec. Rep. 3, var. pag. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037

For the Philippines, length-frequency distributions appearing in the literature have been derived primarily from experimental fishing operations. The troll-caught fish from October 1947 to November 1948 had a range of 34-65 cm with a single mode at 50 cm (Wade 1950). Chikuni (1978) presented length-frequency distributions for fish caught by exploratory purse seine fishing primarily at night in association with rafts ("payao" or "payaw") from November 1974 to June 1977. In Moro Gulf, nearly all of the fish taken were between 40 and 55 cm from January through July. Small fish, 25-35 cm, entered the fishery in May and became more prominent in October and December. In the Sulu Sea, the size range was 30-70 cm in July and a broad mode was centered at 52 cm. The size range was much smaller in May and September, with modes at 62 and 52 cm, respectively. Evans et al.[17] reported length-frequency distributions for both small-scale and commercial fisheries based on Camiguin Island in the Bohol Sea. For handline and various sustenance gear, the size range in March-November 1977 was 37-84 cm TL, with possibly two modes at 66 and 72 cm TL. For commercial ring net boats during the same period, the size range was 18-63 cm TL, but the sample size was too small to determine modes.

For Taiwan, Hu and Yang (1972) collected samples in fresh fish markets from skipjack tuna caught by trolling off the southwest coast between August 1970 and November 1971. The samples ranged from 23 to 71 cm and exhibited modes at 30 and 49 cm.

For Japan, Kawasaki (1952, 1955a, b, 1964, 1965b) used length-frequency distributions for skipjack tuna from various areas in the coastal fishery to separate hypothesized nonmigratory and migratory stocks. The distribution varied considerably among months and areas with respect to both the size range and the number of modes. The total range was from 25 to nearly 80 cm and a distinct mode appeared in every 10 cm interval in at least one time or area stratum. Modes within the 40-60 cm range occurred commonly and often showed a monthly progression in average size. Iwasaki (1976, 1980) determined that the size of fish varied with the means of capture and whether the school was associated with banks, floating debris, birds, and sharks or whales. For fish caught in Japanese waters by bait boats, schools associated with birds had a size range of 20-80 cm with modes at 32, 45, 58, 67, and 75 cm; those associated with banks had a range of 42-62 cm and a single mode at 49 cm; those associated with floating debris had a range of 25-61 cm and modes at 34 and 52 cm; and those with sharks and whales had a range of 33-61 cm and a mode at 50 and possibly 40 cm. For purse seine-caught fish, schools associated with birds had a range of 41-54 cm and a single mode at 45 cm while those associated with floating debris, sharks, or whales had a range of 40-78 cm with modes at 45, 62, and 70 cm.

(b) Indian Ocean

Just as the fisheries are relatively underdeveloped in this ocean compared with the Pacific and Atlantic Oceans, there is likewise less information available on the length composition of the stocks. Marcille and Suzuki (1974) summarized length statistics obtained from Japanese longline operations during the period 1967-71. The size range and modes for each area in the Indian Ocean were as follows: South of Indonesia, 36-86 cm with a single mode at about 50 cm or less; eastern central area, 36-88 cm with two modes at 55 and 64 cm; western central area, 44-78 cm with a mode at 50 cm in the first and second quarters and at 60 cm in the fourth quarter; Bay of Bengal area, 38-84 cm with a single mode generally above 60 cm; and northwestern area, 42-84 cm also with a single, but strong mode usually above 60 cm. Generally there was no indication of a progression of modes with time. With the data combined over all areas, two modes at 55 and 68 cm were apparent.

For the waters of Sri Lanka, Sivasubramaniam (1965) presented figures showing the size composition by coastal area and gear type. For the west coast, troll-caught fish had a range of 20 to 70 cm, with a single mode centered at the 50-55 cm size class. On the east coast, catches by bait boats and trollers had a range of 16 to 70 cm, while for gill net catches, the range was 26 to 70 cm. A single mode occurred in the 51-55 cm interval for all gear types. On the south coast, which is the primary tuna fishing area, the size range was 21 to 80 cm for all gear types, and a single broad mode generally occurred in the 41-45 to 46-50 cm interval. For fish taken in several areas and by various gear types, Sivasubramaniam (1972) found five modal groups at 34-36, 42-44, 52-55, 62-64, and 72-74 cm intervals by using the probability paper method of Harding (1949) and Cassie (1954). For experimental Japanese bait boat fishing, the size range was 28 to 72 cm with modes occurring at 32-34, 44-46, and 58-60 cm intervals (Sivasubramaniam 1975).

For the Indian fishery in the Laccadive Islands from 1958 to 1961, Jones and Silas (1963) reported a size range of 32-72 cm. During the December-April period, two modes at about 48 and 60 cm were observed, while during other months, only the 48 cm mode was apparent. The authors stated that the samples indicate size specific recruitment to the fishery.

For the waters off Madagascar, samples collected during August 1973-March 1975 had a size range of 32-71 cm and a single prominent mode at 49 cm, as well as a less well-defined mode in the 50-55 cm range in some months (Marcille and Stequert 1976). The authors noted that the smaller mode progressed from < 45 cm to just over 50 cm from September 1973 to May 1974, but no progression of modes was evident in the remainder of the time period.

(c) Atlantic Ocean

With the ICCAT emphasizing the description of tuna fisheries and the assessment of the tuna stocks in the Atlantic, a number of papers are now available describing size composition of skipjack tuna. For catches by U.S. purse seiners in the eastern tropical Atlantic during 1968-74, the size range was 25-70 cm (Sakagawa et al. 1976), and a single mode usually occurred at 45-50 cm, though at times two modes at 45 and 50 cm were indicated. For catches by Korean bait boats in the same area in 1975, Choo (1977) presented data showing the ranges of 33-65, 32-62, 31-75, and 36-54 cm in each of the four quarters, or 31-75 cm overall. Quarterly average sizes were stated as 49.8, 48.5, 45.6, and 44.1, or 47.6 cm overall. The size ranges of fish taken by Japanese longline boats in the Northern and Southern Hemispheres were 44-84 and 48-86 cm, respectively, while the only obvious mode occurred at 72 cm in both hemispheres (Kume 1977). For Japanese bait boat catches in the Gulf of Guinea during 1974 and 1975, the size range was found to be 37-62 cm, and few fish below 40 cm were captured (Kikawa and Higashi 1979). Then for Japanese purse seiner catches in the same area during 1967-74, the size range was greater, 22-75 cm, and fish below 40 cm were well represented. The authors indicated that recruitment of 30 cm fish occurred continuously throughout the year. Modal groups were not clearly defined nor was any modal progression apparent. Experimental U.S.S.R. purse seine catches in the eastern Atlantic from 1969 to 1977 consisted of fish with a size range of 28-63 cm and modes occurring in the intervals 36-37, 44-45, and 52-53 cm (Chur et al. 1980). In waters off Brazil, Zavala Camin (1978) reported a size range of 54-78 cm with a mode at about 66 cm for fish taken on tuna longline gear in May-August 1977.

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[17] Evans, L. C., A. D. Uy, and D. D. Tandog. 1978. The abundance, biology and distribution of tuna (Family Thunnidae) in Camiguin and nearby waters. Philippines Dep. Nat. Resour., Bur. Fish. Aquatic Resour., Preliminary Rep., 55 p. Bureau of Fisheries and Aquatic Resources, 860 Quezon Avenue, Quezon City, Metro Manila, Philippines.

Coan (1976) constructed composite length-frequency distributions for fish caught by longline and surface fleets of the participating states over the period 1968-73 (Fig. 64). These distributions were all unimodal with a peak at approximately 50 cm. Sakagawa and Murphy (1976) produced length-frequency distributions comparing the United States purse seine, French-Ivory Coast-Senegalese bait boat, French-Ivory Coast-Senegalese purse seine, and Japanese purse seine fleets. In 1969-71, the distributions for all of these fleets were unimodal with a peak at about 50 cm. In 1972-73, each individual distribution was still unimodal, but the fleets were fishing different sized fish, thus giving the overall distribution a bimodal character with modes at approximately 40 and 55 cm. Length-frequency distributions for specific fleets may be found in Pianet (1974), Bour (1976), Sakagawa et al. (1976), and Ansa-Emmim (1977). For the northwestern Atlantic, Batts (1972a) reported a size range of 26-76 cm for fish taken by charter sportfishing boats off North Carolina, U.S.A., in the summers of 1964 and 1965. He presented length frequencies by age groups (up to five) based on examination of growth rings in the dorsal fin spines, a method generally considered least reliable by recent investigators (see Section 3.43).

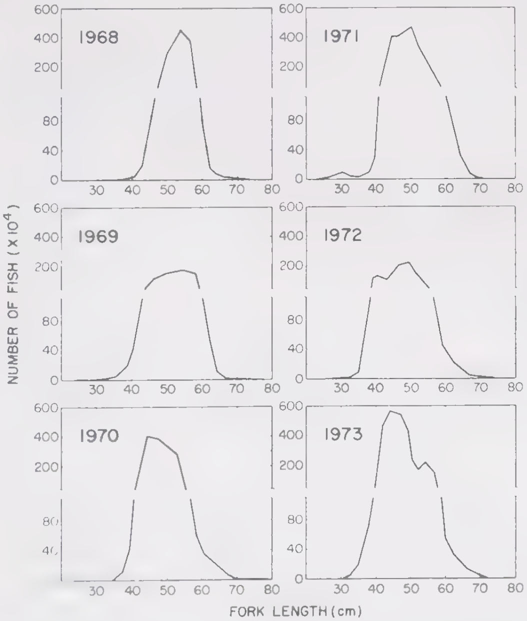

Figure 64.—Length composition of the skipjack tuna catch from the eastern Atlantic Ocean (from Coan 1976).

(2) Size at first capture

The size at first capture of fish amounting to significant numbers in most years in most fisheries, is about 40 cm. Recruitment into the fishable stocks generally takes place at a smaller size, around 30 or even 25 cm for many fisheries (Kawasaki 1955a, 1964; Sivasubramaniam 1965, 1972; Hu and Yang 1972; Iwasaki 1976, 1980; Marcille and Stequert 1976; Sakagawa et al. 1976; Choo 1977; Habib 1978; Honma and Suzuki 1978; Kikawa and Higashi 1979; Habib et al. 1980a, b, c; Tanaka undated a, b, c, 1978, 1979, 1980; Tohoku Regional Fisheries Research Laboratory undated a, b, c, d). For the ring net and purse seine fisheries in the Philippines, the size at first capture is around 25 cm and the size at recruitment is around 15 cm (Evans et al. footnote 17; Choo[18]).

(3) Size at maturity

See Section 3.12.

(4) Length-weight relationships

Length-weight relationships have now been published for all oceans (Table 17), but they are not available for all fisheries. Neither have the papers cited below included studies of sexual, seasonal, or long-term variations.

All of the studies cited in Table 17 fitted the allometric growth equation $W = bL^a$ where W is weight in grams, kilograms, or pounds, L is usually fork length in centimeters or millimeters, a is the coefficient of allometry, and b is another constant. In all but one of the cited studies, the log-linear transformation of the equation,

$$\log_e W = \log_e b + a \log_e L$$

was used to estimate the parameters using predictive (linear) regression analysis. Today it is generally believed that the length-weight relationship is intrinsically nonlinear, meaning

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[18] Choo, Woo-Il. Undated. Interim report on tuna sampling project in the Philippines and Indonesia, November 1979-February 1980. Unpubl. rep. U.N. South China Sea Fish. Develop. Coord. Prog., no pag. Korea Rural Economics Institute, Fishery Development and Research Division, 4-102 Hoigi-dong, Dongdaemoo-ku, Seoul, Korea

Table 17.—Length-weight relationships of skipjack tuna.

Source	Locality	No. of fish	Size range (cm)	Constant *b*	Coefficient of allometry *a*	Weight unit	Length unit	Calculated weight of 55 cm fish (kg)	Comments
Uda (1941)	Bonin Is. W. Pacific	268	27-69	0.205	3.67	g	cm FL	449.9	Columns 4 and 9 estimated from Uda's fig. 6. Regression statistics suspect.
Kawasaki (1952)	NE of Japan	20	30-60	0.0113	3.16	g	cm FL	3.57	Bait boat catches.
Tester and Nakamura (1957)	Hawaii	268	39-83	1.878×10^{-5}	3.2164	lb	cm FL	3.37	Size range calculated.
Chatwin (1959)	E. Pacific	924	39-71	3.652×10^{-9}	3.403	lb	mm FL	3.50	Bait boat and purse seine catches.
Hennemuth (1959)	E. Pacific	1,282	39-71	3.763×10^{-9}	3.265	lb	mm FL	3.58	Includes data from Chatwin (1959).
Ronquillo (1963)	Philippines	189	34-66	3.267×10^{-5}	3.09569	lb	cm TL	3.40	Males only. Data from Ronquillo's fig. 25 and regression equations.
Ronquillo (1963)	Philippines	151	34-63	1.976×10^{-5}	2.96482	lb	cm TL	3.33	Females only. Data from Ronquillo's fig. 25 and regression equations.
Nakamura and Uchiyama (1966)	Hawaii	1,298	33-88	4.546×10^{-9}	3.36836	lb	mm FL	3.50	Bait boat catches.
Batts (1972a)	W. Atlantic	644	26-76	2.560×10^{-9}	3.3533	kg	mm FL	3.33	Troll catches.
Lenarz (1974)	E. Atlantic	2,554	36-64	5.611×10^{-6}	3.31497	kg	cm FL	3.30	Log linear regression analysis.
Pianet (1974)	E. Atlantic	520	40-73	4.115×10^{-5}	3.409	kg	cm FL	3.35	Linear regression analysis.
Marcille and Stequert (1976)	Madagascar	848	41-62	1.131×10^{-5}	3.158	kg	cm FL	3.54	Bait boat catches.
Vooren (1976)	New Zealand	100	35-54	6.206×10^{-6}	3.19	g	mm FL	3.35	Purse seine catches.
Evans et al. (text footnote 17)	Philippines	200	48-85	5.500×10^{-4}	2.20	kg	cm TL	3.71	Handline catches.
Evans et al. (text footnote 17)	Philippines	44	17-62	3.727×10^{-3}	1.70	kg	cm TL	3.39	Artisanal fishing gears.
Habib (1978)	New Zealand	120	38-71	3.475×10^{-6}	3.29	g	mm FL	3.60	Purse seine catches.

that parameters estimated from a log-linearized relationship are biased. Corrective procedures are available, but none were employed in the papers cited. In addition, Ricker (1973) has pointed out that the predictive regression method (which assumes a dependent-independent variable situation) tends to produce inflated estimates of *a*, especially when the sample range truncates that of the true population; a geometric mean functional (reduced major axis) regression (which does not assume a dependent-independent variable situation) produces less biased results. Pianet (1974) used the latter procedure but performed it on log-transformed data.

A summary of these studies is presented in Table 17, and a typical curve describing the relationship is given in Figure 65. The table is an updated version of a similar table presented by Nakamura and Uchiyama (1966), and the figure, based on data from the central Pacific containing the largest sample size and widest size range of all studies cited, was taken from the same reference. The calculated weights of fish of a common size, based on the regression statistics of the various authors, show close agreement except for that obtained by Uda (1941). The estimates of the coefficients of allometry are amazingly similar, except for those published by Evans et al. (footnote 17), and no effect of ocean or gear type is apparent.

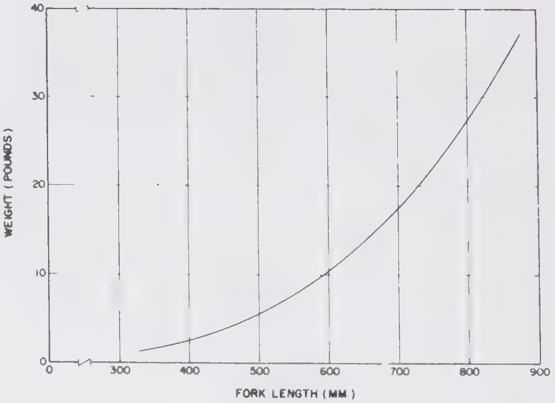

Figure 65.—Length-weight relation of skipjack tuna: log weight = −8.34241 + 3.36836 log length (parameters not corrected for transformation bias); number of observations, 1,298; size range, 327-877 mm; data collection period February 1948-December 1960; from files of Southwest Fisheries Center (from Nakamura and Uchiyama 1966).

4.2 Abundance and density (of population)

(1) Pacific Ocean

Forsbergh (1980) has recently reviewed the history of the measurement of apparent abundance of skipjack tuna in the eastern tropical Pacific. Shimada and Schaefer (1956) produced the first measure of relative density by comparing the daily catch rates of bait boats standardized by vessel class. They concluded from the trends shown in Figure 66 that the fishery was having no measurable effect on the stock. Since purse seine vessels have almost entirely replaced bait boats in the fishery, the measure used today is reported catch divided by reported fishing effort standardized to class 3 purse seine vessels (101-200 short tons or 94-181 t of carrying capacity). For a later period, 1960-79 (Fig. 67), the index in terms of purse seine units shows considerable annual variation but again no discernible trend.

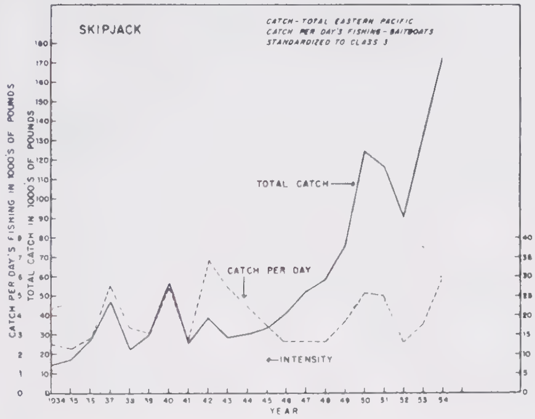

Figure 66.—Catch per standardized-day fished, total catch, and calculated relative fishing intensity for skipjack tuna in the eastern Pacific Ocean, 1934-54 (from Shimada and Schaefer 1956).

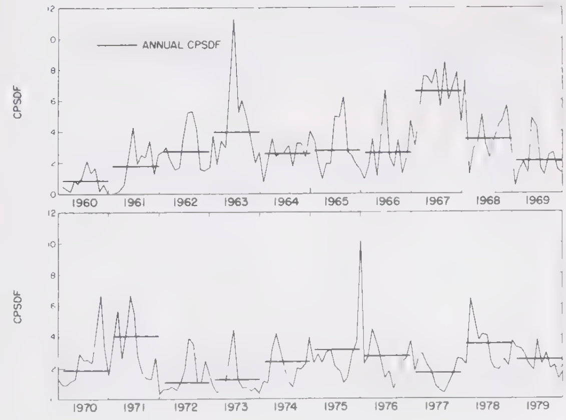

Figure 67.—Monthly and annual catch per standard day's fishing (CPSDF) for skipjack tuna, in class 3 purse seine units, in the eastern tropical Pacific during 1960-79 (from Forsbergh 1980).

Since some fishing effort directed primarily at yellowfin tuna is included in the calculation, this index is biased. Several attempts have been made to improve the index. Calkins (1961) and then Joseph and Calkins (1969) calculated relative density after eliminating those areas of low skipjack tuna catch where the fishing effort was directed primarily at yellowfin tuna. The resultant index of relative abundance again did not show a long-term trend over the 1951-65 period. Relative density was highest in the third quarter, and there appeared to be no relationship between the indices in the areas north and south of lat. 15°N. Subsequently, Pella and Psaropulos (1975) adjusted the fishing effort statistics by simulating the effect of the following factors on the fishing power of vessels: Vessel speed, probability of capturing sighted tuna schools, time spent in a set, and portions of schools retained that are set upon successfully. Using a new standardized fishing effort statistic based on their simulation, they found a different history of relative stock abundance over the years of the fishery (Fig. 68). There seems to be some indication of a decrease in abundance of skipjack tuna in the northern grounds and a definite decrease in the southern grounds. It is not known at this time which index of abundance is the better descriptor of the stock(s). Later, the IATTC computed relative abundance using only those 5° latitude by 5° longitude areas and 3-mo periods where 200 short tons (181 t) or more of skipjack tuna were caught and 100 or more standardized fishing days were expended. This procedure retained 89% of the catch and eliminated 43% of the purse seine fishing effort in 1961-79. The resulting indices of fish density for the years 1951-79 (Fig. 69) show no clear trend in the areas north of lat. 15°N and between lat. 15° and 5°N, whereas south of lat. 5°N the trend has a convex shape (Forsbergh 1980).

For the bait boat fishery in Hawaii, a number of estimates of relative abundance have been made. These indices, measured in catch per trip or per effective trip (as in Fig. 70), are highly correlated with catch and show no long-term trend (Yamashita 1958; Shippen 1961; Uchida 1967, 1976). A

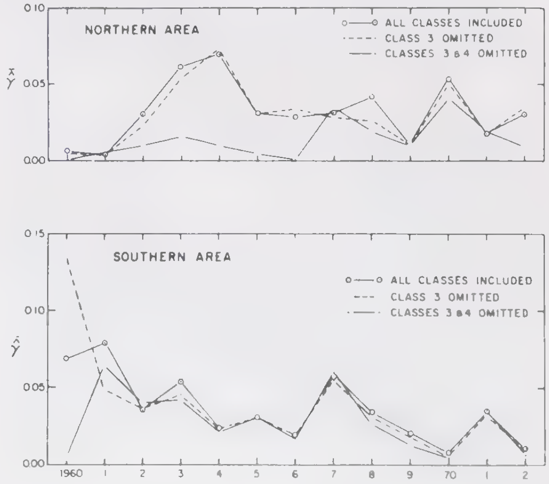

Figure 68.—Annual biomass indices of skipjack tuna in the traditional fishing areas of the eastern Pacific Ocean using different combinations of vessel classes, 1960-72 (from Pella and Psaropulos 1975).

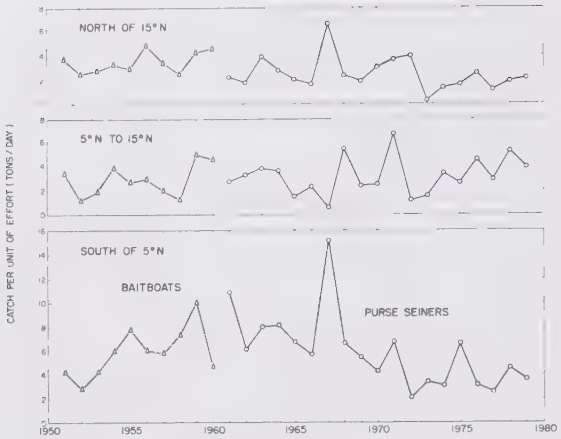

Figure 69.—Indices of abundance of skipjack tuna (in tons per day's fishing standardized to class 4 bait boats and class 3 purse seiners) for three areas of the eastern Pacific Ocean (from Forsbergh 1980).

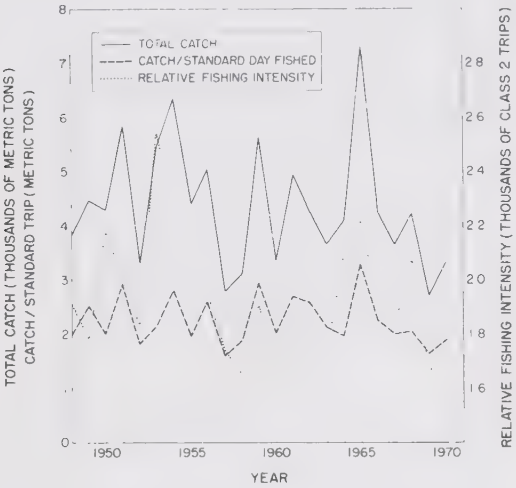

Figure 70.—Total catch, catch per standard day fished, and the relative fishing intensity of skipjack tuna taken in the Hawaiian fishery, 1948-70 (from Uchida 1976).

marked seasonal trend is quite apparent with the highest values occurring in May-September (Shippen 1961).

For the purse seine fishery in New Zealand, relative abundance in terms of catch per set, catch per effective set, catch per day, and catch per season-day shows no long-term trend over the 1975-76 through 1979-80 seasons (Habib 1976, 1978; Habib et al. 1980a, b, c). As in Hawaii, there is a marked seasonal trend, but with the highest density occurring in the January-February period.

In Papua New Guinea for the locally based bait boat fishery, Wankowski (1980) presented relative abundance indices showing the highest values occurring in May-September and the lowest values occurring in December-February. No long-term trend for the period 1970-79 was apparent.

In the Japanese southern water fishery (south of lat. 24°N and from long. 125°E to 150°W), catch per vessel increased both for the 1958-68 period in the Bonin-northern Mariana Islands area (Iwasaki 1970) and for 1964-75 over the entire fishery (Kasahara 1977). However, this trend probably reflects the evolution to larger boats in the fleet rather than changes in relative population density. While catch per day for some areas in the southern water bait boat fishery (Fig. 71) has shown a declining trend (Kasahara 1971), a similar index derived from Japanese purse seine operations in tropical waters shows no such trend (Honma and Suzuki 1978).

For the bait boat fishery off the northeast coast of Japan in 1951-62 (Kawasaki 1964) and off the south and southwest coast in 1957-69 (Kasahara 1971), no trend in relative abundance was evident. The same was true for the purse seine fishery in coastal waters from 1971 to 1974 (Honma and Suzuki 1978). However, Kasahara (1975) showed that the relative density has declined with increasing fishing effort in the Japanese coastal fishery during the period 1958-72. There is a regular seasonal cycle in relative abundance with the highest values occurring in June-August (Anraku and Kawasaki 1966). Lastly, Ishida (1975) showed that there was no

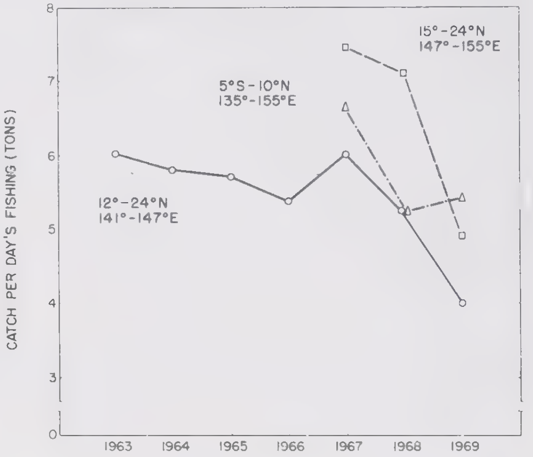

Figure 71.—Indices of relative abundance for the fishing season May-October of skipjack tuna in the Japanese southern water fishery, 1963-69 (from Kasahara 1971).

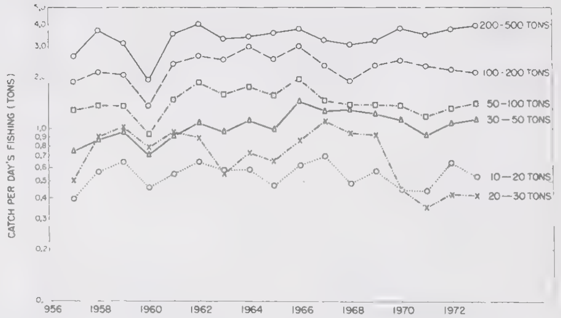

Figure 72.—Catch per day for Japanese bait boats of various size classes in the western Pacific (from Ishida 1975).

trend in the catch per day of Japanese bait boats from 1957 to 1973, apparently over all western Pacific fishery grounds (Fig. 72).

(2) Atlantic Ocean

A number of estimates of relative abundance have been determined using data from the surface fishery in the eastern tropical Atlantic. As is the case with the eastern tropical Pacific fishery, this is a two-species fishery and similar problems exist in separating fishing effort directed at skipjack and yellowfin tunas. For the local bait boat fishery in Angola, de Campos Rosado (1971) presented data showing a steady index of relative abundance for both species combined, while the index for yellowfin tuna has declined proportionally to the increase in the index for skipjack tuna. The relative density derived from purse seine fishing showed an increase in the last half of the year for both United States and Japanese vessels (Sakagawa 1974; Kikawa and Higashi 1979). However, no consistent seasonality in the catch per day statistics for Japanese bait boats was apparent (Kume 1978; Kikawa and Higashi 1979). None of these studies, nor Fonteneau and Cayre's (1980) study on the French-Ivory Coast-Senegalese purse seine fleets, found a long-term trend in relative abundance. However, a study by Pianet (1980) utilizing data from French-Ivory Coast-Senegalese, United States, and Japanese bait boat and purse seine fleets did find a slight decline in relative density over the 1969-78 period (Fig. 73).

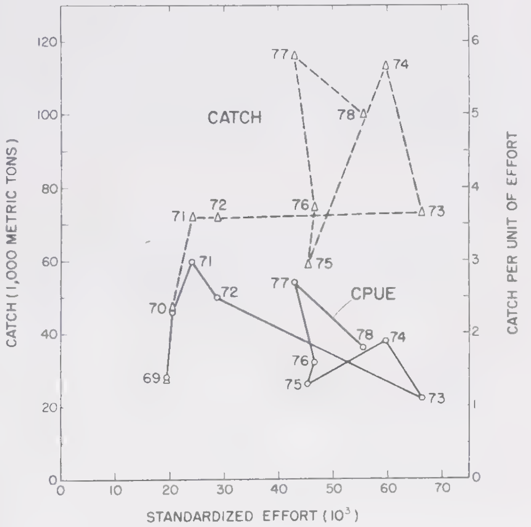

Figure 73.—Relation between catch and CPUE versus standardized effort in the eastern Atlantic (m = 2, K = 1) (from Pianet 1980).

4.3 Natality and recruitment

Various factors relating to natality were discussed in Section 3.1. Reproduction, and more specifically fecundity, was covered in Section 3.15. Recruitment into a fishery, in terms of migration, was discussed in Section 3.51.

Since recruitment into the established and major fisheries around the world is extremely variable, much speculation has been voiced about recruitment into the population(s), but little actual research has been reported in the literature. Recently Forsbergh (1980) described work carried out on this subject by the IATTC in the eastern tropical Pacific. An index of relative abundance of young skipjack tuna in the fishery was tested against three factors: Sea surface temperature in an hypothesized spawning area in the central tropical Pacific (long. 130°W-180°) approximately 1.5 yr earlier, barometric pressure differences at stations in the Indian and Pacific Oceans, and a mixing index in the spawning area. While a significant relationship was found between relative abundance of skipjack tuna in the fishery and temperature in the central tropical Pacific (IATTC 1972, 1973), no obvious biological explanation for this relationship was apparent. Subsequently it was found that the temperature variations in the spawning area were correlated with the southern oscillation index. This index, which is defined as the difference between sea-level atmospheric pressure at sites located in the Indonesian equatorial low region and those in the South Pacific subtropical high region, has been used to study large-scale variations in meteorological and oceanographic conditions occurring over the equatorial Pacific, including the El Niño phenomenon off the northwest coast of South America (Quinn 1976, 1977). In turn, the southern oscillation index has been found to be related to wind conditions in the central equatorial Pacific. During the same period Lasker (1975, 1978, 1981) showed that the survival of anchovy larvae in the California Current was dependent in part on the availability of sufficiently concentrated food and that this occurred with stable structuring of the upper mixed layer of inshore waters. During periods of high wind or strong upwelling, this stable structuring is destroyed and food organisms are dispersed throughout the upper mixed layer resulting in too low a concentration for survival of anchovy larvae. Hypothesizing a similar phenomenon with respect to the survival of skipjack tuna larvae in the central equatorial Pacific spawning area, a significant correlation was found between the index of abundance of fish between 12 and 24 mo of age in the eastern tropical Pacific fishery and an index of mixing (the curl or cube of the wind speed) in the central Pacific approximately 1.5 yr earlier. While the relationship is statistically significant, it accounts for only 47% of the variation and is thus a poor predictor of catch.

4.4 Mortality and morbidity

Most estimates of mortality coefficients appearing in the literature have been calculated for the stock in the eastern tropical Pacific. Using tagging data from 1957, Fink (1965) estimated the total mortality coefficient *Z* to be 6.98, the fishing mortality coefficient *F* to be 2.10, and, using a value of 1.06 for mortality due to tagging from work on yellowfin tuna, the coefficient of natural mortality *M* to be 3.82, all on an annual basis. Joseph and Calkins (1969), using tagging data from a later period, estimated *M* on an annual basis as 1.68. Again utilizing more tagging data for the eastern tropical Pacific, Bayliff[19] estimated *Z* to be 0.58, *F* to be 0.35, and *M* to be 0.23, but in this case, on a monthly basis. Using a completely different approach, Silliman (1966) simulated a catch history for the eastern tropical Pacific fishery by allowing *M* to vary from 0.2 to 0.7 and holding *Z* constant at 0.8. The best fit was obtained with *M* at 0.3, but this method does not provide a unique solution. Most authors indicated that their estimates should be considered as preliminary and acknowledged that the estimates of *M* included emigration and losses due to tagging. Considering the lifespan of skipjack tuna to be about 5 yr, Murphy and Sakagawa (1977) stated that the published estimates of *M* were either too low (0.3) or too high (1.68 and 3.82).

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[19] Bayliff, W. H. 1977. Estimates of the rates of mortality of skipjack tuna in the eastern Pacific Ocean derived from tagging experiments. Inter-Am. Trop. Tuna Comm., Internal Rep. 10, 59 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037

Using tagging data for 1973-74 in Papua New Guinea, Lewis (1980) estimated *Z* on a monthly basis as being equal to 0.257 overall and 1.285 when the stock was exposed to the fishery. Lewis also pointed out that the estimates of *Z* included emigration.

4.5 Dynamics of population (as a whole)

Assessments of the state of the stocks are currently available for the Atlantic and the eastern Pacific, while estimates of potential production are available for the western Pacific and the Indian Oceans. Most of the results must be viewed as preliminary because of the highly variable relationship between catch per unit effort and effort, as well as the low reliability of estimates of population parameters.

(1) Atlantic Ocean

Two estimates of the potential yield are available. First, Shomura (1966b) argued that since the Atlantic Ocean is half the size of the Pacific Ocean, the potential yield for the Atlantic should be half that for the more well-developed fisheries in the Pacific Ocean. Using a catch of 234,100 t in 1962 for the Pacific, he estimated the potential yield for the Atlantic to be 117,000 t, whereas using the largest reported catch for the Pacific, 662,000 t in 1978 (FAO 1980), results in an estimate of 331,000 t for the Atlantic. The harvest reported for the entire Atlantic Ocean was 87,714 t in 1979 (FAO 1980). [Japan.] Fisheries Agency[20] estimated a total production of 100,000 t for the North Atlantic and 100,000-150,000 t for the South Atlantic. The method was based on the abundance of skipjack tuna larvae compared with that for other commercial tuna species.

A yield-per-recruit analysis of the eastern tropical Atlantic fishery by Hayasi (1974) indicated an optimum size at first capture of 0.6-1.3 kg (about 33-40 cm). Hayasi concluded that there was no evidence that skipjack tuna in the Atlantic Ocean was fully exploited. Sakagawa and Murphy (1976) examined the relationship between total catch and normalized catch per unit effort for several gear types in the eastern tropical Atlantic. They concluded also that the stocks were not being fully exploited since there was no consistent trend in the data. Recently, Pianet (1980) found a slight but apparently significant decline in catch per unit effort versus effort for standardized French-Ivory Coast-Senegalese, United States, and Japanese bait boat and purse seiner data from 1969 to 1978 (Fig. 73). A production model fitted to these data resulted in an estimate for maximum sustainable yield of 92,500 t for the eastern tropical Atlantic.

(2) Pacific Ocean

In the eastern tropical Pacific, Joseph and Calkins (1969) estimated yield per recruit, using the Ricker (1958) model, for both the northern and southern skipjack tuna fisheries (Fig. 74). Their model assumed that all individuals in the stock make two passes through the fisheries, and it included von Bertalanffy growth parameters and mortality estimates derived in the same paper. From Figure 74, it can be seen that the yield per recruit for the northern fishery could be increased only slightly by a doubling of the fishing effort (a multiplier equal to 1.0 represents the level of fishing mortality in 1963), while that for the southern fishery could be increased 1 to 1.5 times by increasing fishing effort 2 to 2.5 times.

Rothschild (1966) and Silliman (1966) both estimated the potential yield for the combined eastern Pacific stocks if they were harvested beyond the range of the existing fishery. Using the Beverton and Holt (1957) yield per recruit model and lengths of time exposed to the existing coastal fishery of 2 and 6 mo (Fig. 75), Rothschild estimated the yield could be increased between 2 and 17 times the then existing catch. Silliman (1966) estimated the potential yield using a population simulation model which held the total mortality coeffi-

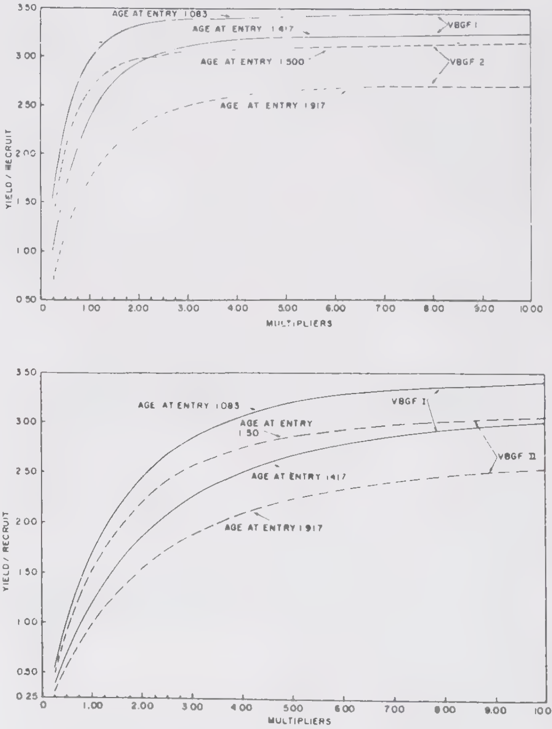

Figure 74.—Yield per recruit of skipjack tuna at age of entry into the northern fishery (top) and southern fishery (bottom), eastern Pacific Ocean, using von Bertalanffy growth parameters from ungrouped data (VBGF 1) and grouped data (VBGF 2) (from Joseph and Calkins 1969).

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[20] [Japan.] Fisheries Agency. 1968. On the possibility of developing marine fishery resources. Information, cited in Kawasaki 1972.

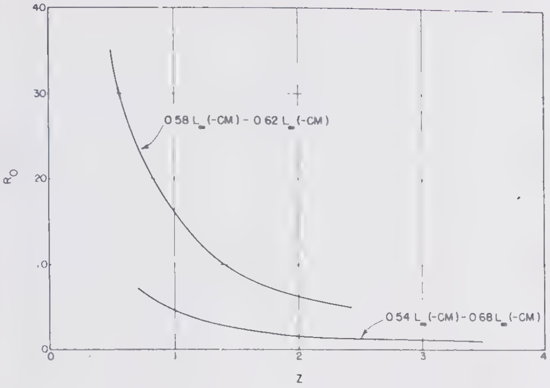

Figure 75.—Values of R_0 (ratio of yields under whole-life exploitation to yield under limited-life exploitation) for skipjack tuna, as a function of *Z* between 1 and 2. Upper curve is for assumed sojourn time of 2 mo, lower curve for 6 mo (from Rothschild 1966).

cient *Z* constant at 0.8 and allowed the natural mortality coefficient *M* to vary from 0.2 to 0.7. Maximum sustainable yield was estimated as 225,000 t with *M* equal to 0.3 (Table 18). If Rothschild's (1966) estimate of maximum length of skipjack tuna is conservative and if the escapement stock from the eastern Pacific fishery is only a segment of the total fish available in the central Pacific, both of which are likely, then both Rothschild and Silliman underestimated the potential yield from the central Pacific. While the results from both these authors suggest that yield could be increased by harvesting the escapement stock from the coastal fishery, Joseph and Calkins (1969) observed that yield per recruit could be increased by harvesting fish younger than were then available to the fleet in the eastern tropical Pacific.

Table 18.—Estimates of sustainable yield for the eastern-central Pacific stock of skipjack tuna at *M* of 0.03 and at selected values of *F* (from Silliman 1966).

F	Average sustainable yield (1,000 t)	Effort[1] 1,000 boat-days from $f = \frac{F}{q}$	Tons/boat-day
0.5	180	33	5.5
0.6	200	40	5.0
0.8	220	53	4.2
0.9	220	60	3.7
1.0	225	67	3.4
1.1	215	73	2.9

[1] $q = 0.01501$ from $\bar{F} = 0.5$ and $f = 33.3$, for 1952-56.

[Japan.] Fisheries Agency (footnote 20) estimated potential yields for various oceans and subareas based on the abundance of skipjack tuna larvae and juveniles and their occurrence in the stomachs of predators. These estimates are:

Japanese coastal area	Increase of 200,000-400,000 t
Entire Pacific Ocean	Increase to 800,000-1,000,000 t
Indian Ocean	200,000-300,000 t.

Suda (1972) elaborated on the above procedure by saying that since about twice the number of skipjack tuna larvae were taken in plankton tows as larvae of all other commercial tunas, the spawning stock of skipjack tuna was also roughly two times that of other commercial tunas. Therefore, the potential production of skipjack tuna should be at least two times more than that of all other commercial tunas. Both Kawasaki (1972) and Matsumoto (1974) noted that Suda's projections of adult skipjack tuna catch from larval abundance was oversimplified. By citing differences in fecundity and average body sizes between skipjack tuna and other tunas, Matsumoto showed that the conversion ratio of 2:1 in favor of the skipjack tuna was not logical. One other important factor not taken into account by Suda was the difference in the efficiency of the different types of fishing gear used in taking the various species of tunas and the effect this would have on the conversion ratio.

4.6 The population in the community and the ecosystem

4.61 Physical features of the biotope of the community

Skipjack tuna inhabit the epipelagic zone of the world's major oceans and apparently only make forages into deeper zones. As such, they generally live in the upper mixed layer where temperature and salinity variations are small and where oxygen is at or near saturation. Latitudinal and longitudinal variations in temperature and depth of the mixed layer determine to a great extent the distribution of the several races of skipjack tuna. The greatest concentrations of fishery vulnerable skipjack tuna are limited to the temperature range 17°-28°C. The major water masses and their associated currents also influence the distribution of the species, not only through drift of the larvae and possibly the adults as well, but also through the availability of food associated with current boundaries and areas of upwelling. Except for these latter areas of higher productivity, the epipelagic zone is characterized by low productivity.

4.62 Species composition of the community

The most important or obvious members of the community are the permanent members of the nekton that feed and reproduce in the epipelagic zone. These include some sharks, *Lamna nasus*, *L. ditropis*, *Isurus glaucus*, *Cetorhinus maximus*, *Prionace glauca*, *Pterolamiops longimanus*, and others; many flying fishes, *Exocoetus volitans*, *E. obtusirostris*, *E. monocirrhus*, *Hirundichthys speculiger*, *H. rondeletii*, *H. albimaculatus*, *Prognichthys gibbifrons*, *P. sealei*, and others; all the Scomberesocidae; several Scombridae, *Gasterochisma melampus*, *Allothunnus fallai*, *Thunnus alalunga*, *T. albacares*, *T. obesus*; marlins, *Tetrapturus audax*, *T. albidus*, *T. angustirostris*, *Makaira nigricans*; swordfish, *Xiphias gladius*; the dolphin, *Coryphaena equiselis*; opah, *Lampris regius*; all the Bramidae; many Nomeidae and Centrolophidae, *Nomeus albula*; species of genera *Psenes*, *Cubiceps*, *Schedophilus*, *Centrolophus*, and *Ichichthys*; Molidae; and some others. A second group of nekton includes those fish that spend their adult stages in the epipelagic zone but whose egg and juvenile stages are found elsewhere. These include the whale shark, *Rhincodon typus*; the dolphin; bluefin tuna, *Thunnus thynnus*; some halfbeaks (Family Hemiramphidae) of the genus *Euleptorhamphus*; needlefishes (Family Belonidae) of the genera *Platybelone* and *Ablennes*; and flyingfishes (Exocoetidae) of the genera *Cypselurus* and *Cheilopogon*. A third group includes the eggs, larvae, and juvenile stages of fishes that inhabit the neritic (pelagic and littoral zones) and the abyssal zones. Among these are some Atherinidae, Scombridae, Carangidae, Gonorhynchidae, Synodontidae, Holocentridae, Stichaeidae, Mullidae, Scorpaenidae, Hexagrammidae, Cottidae (Hemilepidotinae), Nototheniidae, Chaenichthyidae, Acanthuridae, Bothidae, Cynoglossidae, Pleuronectidae, Gonostomidae (*Cyclothone, Vinciguerria*), anglerfishes (Ceratioidei), and apparently some lanternfishes (Myctophidae). Also present are some mesopelagic species that migrate into the epipelagic zone during the night. These include the sharks, *Euprotomicrus bispinatus* and probably *Isistius brasiliensis*; the snake mackerel, *Gempylus serpens*; subsurface lanternfishes of the genera *Myctophum, Symbolophorus, Centrobranchus, Gonichthys, Tarletonbeania, Hygophum, Loweina*; a few members of Families Melanostomiatidae (*Photonectes, Echiostoma*); and Astronesthidae (*Astronesthes*); and others (Parin 1968).

4.63 Interrelations of the population of the species in the community and ecosystem

Waldron (1963) has adequately described the position of the skipjack tuna as follows: "Within the marine community the skipjack may be listed both as prey and predator, although as a large adult it may be only one step removed from a climax predator. In its larval and juvenile stages it serves as food for larger fish, including adult skipjack. As an adult it serves as food for larger tunas and spearfishes, and at the same time preys upon small to moderate-sized pelagic crustaceans, molluscs, and fish. Skipjack compete for food with tunas and other fish of similar size and habits. They might even be considered as competing with sea birds, for the food organisms are often apparently driven to the surface of the water, where they are preyed upon by both skipjack and various sea birds."

4.64 Hypothetical habitat of skipjack tuna

Metabolic and physiological properties of skipjack tuna in relation to the environment have been discussed in Section 3.63.

5 EXPLOITATION

5.1 Fishing equipment

The two most productive means of catching skipjack tuna on a worldwide basis have been pole-and-line and purse seine fishing. Other methods include gill netting, trolling, trap fishing, harpooning, and beach seining. Recently the importance of flotsam or man-made aggregation devices has increased greatly. Likewise, aerial spotting has become common in some fisheries, and the application of remote sensing is being investigated.

The pole-and-line, bait boat, or live bait fishing method is or has been employed by Japanese fishermen throughout the Pacific and off both coasts of Africa, and by the United States, Ecuadorian, Maldivian, Korean, and Indonesian fishermen, to name only the most obvious instances. Generally, the gear consists of a bamboo pole varying from 3 to 6 m although fiberglass is sometimes used now. The length of the line varies depending on the distance of the fishing location from the sea surface. Generally, a barbless, artificial lure is used which is designed to imitate either a baitfish or a squid. The design of the bait boats varies considerably depending on the nationality and much effort has been expended in recent years, particularly by the Japanese, in modernizing the boats. Cleaver and Shimada (1950) and Yoshida (1966) provided descriptions of the boats that were in use a number of years ago in Japan and the United States. Descriptions of 200 and 250 gross tons (GT) Japanese bait boats appear in Kearney and Hallier (1980b). More modern bait boats are equipped with baitwells with recirculating or even refrigerated water, automatic fishing poles, and fish finders.

Because the Japanese style bait boat carries more fishermen than other types (over 35 compared with as few as 6) and, thus, experiences problems in obtaining enough qualified fishermen, the Japanese have been experimenting with automatic gear, such as a continuous circulating mainline with hooks on short droppers (Inoue 1966; Igeta et al. 1978) and mechanical pole machines (Iwashita et al. 1967; Suzuki Tekkojo Kabushiki Kaisha[21]). The automatic pole machines are now used on 80% of the Japanese bait boats larger than 200 GT, but not on the narrow but highly productive bow area (Maruyama 1980). These machines have also been tried in Australia, as well as in Hawaii and the west coast of the United States.

As the name implies, bait boat fishing includes the chumming of live bait to attract and hold tuna schools close to the vessel. Thus, bait boat fishing is essentially a double fishery, where suitable baitfish resources must be found, captured, hardened for future use, and transported to the fishing grounds in baitwells of the fishing boats. In addition to these technical aspects of baitfishing, the ability of baitfish stocks to withstand harvesting pressure has been investigated by Bayliff (1967) for the eastern tropical Pacific, Wetherall (1977) for Hawaii, and Dalzell and Wankowski (1980) for Papua New Guinea. Because of the limited availability of natural baitfish supplies in small island areas, some interest has been shown in raising or culturing baitfish (Baldwin 1975, 1977; Gopalakrishnan 1979). A workshop on baitfish has covered many of these subjects (Shomura 1977).

Advantages of bait boat fishing are the relatively small capital investment involved, ability to harvest small schools of fish, ability to operate out of small ports with a minimum of technical support, and ability to utilize unskilled labor. The major disadvantage is that it is a double fishery. Other disadvantages include the size of the fishing crew, dependence on the biting behavior of the tuna schools, and dependence on good weather conditions to find and fish tuna schools.

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[21] Suzuki Tekkojo Kabushiki Kaisha. 1970. Report on the development of an automatic skipjack fishing machine. From a mimeographed report by the Suzuki Tekkojo Kabushiki Kaisha (Suzuki Ironworks Co., Ltd.), Ishinomaki, Miyagi, Japan, Sept. 30, 1970. [Engl. transl. by T. Otsu, 1970. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.]

Purse seine fishing for tunas began in the eastern tropical Pacific in the 1950's when many of the bait boat clippers began converting to purse seine gear (McNeely 1961). The development of the Puretic power block, which lifts the net with its float line and purse rings, thus enabling the net to be stacked on the deck for the next set, made this possible. Technical aspects of the purse seine are described in McNeely (1961) and Green et al. (1971). Newer developments include lighter fabrication of the net to allow for greater length and depth and other modifications to increase the survival of porpoise (Coe and Vergne 1977). The purse seine net is basically a long net that is set around a school. The ends are brought together and the purse line is drawn until the bottom of the net is pursed or closed. While the first U.S. purse seiners in the eastern tropical Pacific were as small as 130 GT, they now are much larger, commonly around 1,000 GT and as large as 2,000 GT. Modern purse seiners carry a full complement of electronic gear including fish finders and satellite navigation equipment. Similar vessels are now being built in several American countries (e.g., United States, Mexico, and Peru), Spain, France, Poland, and Japan. Fishing operations have expanded from the eastern tropical Pacific to the western Pacific including off Japan, Trust Territory of the Pacific Islands, Philippines, Papua New Guinea, and New Zealand. The more successful boats in the open ocean or small island areas of the western Pacific tend to be smaller, averaging around 500 GT, than in the eastern tropical Pacific. A substantial purse seine fishery takes place in the eastern tropical Atlantic, and the principal countries in the fishery are France, Spain, United States, Japan, and U.S.S.R. Exploratory fishing has taken place in the Indian Ocean.

Both bait boats and purse seine operations have traditionally depended on the spotting of free-swimming, bird-associated, or flotsam-associated tuna schools from the bridge or crow's nest of the fishing boats. Many large purse seine boats now carry helicopters to search for fish schools, and land-based airplanes are commonly used in some fisheries, e.g., in New Zealand (Bell 1976; Habib[22]). Attempts are now underway to use remote sensing of sea surface temperature gradients from satellites or aircraft as an indication of likely fishing areas (Evans 1977; Stevenson and Miller 1977; Eggleston and Paul 1978; Noel 1978; Petit[23,24]; Petit et al. [25]).

While the association of skipjack tuna schools with flotsam (including whales and large sharks) has been known for some time (Inoue et al. 1963, 1968a, b; Greenblatt 1979) and exploited by both bait boats and purse seiners, the new purse seine fishery in the equatorial western Pacific is very dependent on this association. Most purse seine sets take place either at dusk or dawn. Also, anchored rafts are now employed on a commercial scale in the Philippines (Aprieto 1980, 1981; Matsumoto footnote 12) and in Hawaii (Matsumoto et al. 1981), and they are being deployed experimentally throughout the South Pacific, e.g., in American Samoa, West Samoa, northern Marianas, Guam, Palau Islands, Cook Island, and Tonga (Matsumoto footnote 12); in the eastern Pacific (Guillen and Bratten[26]); and in the Indian Ocean, for example, in the Maldives; and probably in other areas as well. In the Philippines, small scouting boats or canoes are used to determine whether tuna have been attracted to the rafts. If so, a light skiff ties up to the raft (or payao) to concentrate the fish for seining. The lights used vary from gasoline lanterns to powerful electrical lights, either submerged or above the surface, depending on the size of the operation. When it is determined that the fish are sufficiently concentrated around the light boat and the raft, the light boat is allowed to slowly drift away until there is room to set the purse seine around the light boat without becoming entangled in the raft. A given purse seiner, which can be anything from a converted tuna longliner to a 2,000 GT purse seiner, will use 15 or more rafts, setting up to 3 times a night and averaging a little over 1 set per night. Tuna are caught on over 90% of the sets.

Advantages of purse seine fishing are independence from baitfish resources, lower requirements for shipboard manpower, and highly efficient catch rate per man per vessel. Disadvantages include the size of the capital investment, inability to fish in rough waters, inability (currently) to fish during the day in waters with a deep thermocline, the requirement for sophisticated unloading and support facilities, and large fuel consumption except when using anchored rafts.

Gill nets are the primary gear used to catch tuna in Sri Lanka and Somalia. The gear used in Sri Lanka is described in de Bruin (1970) and Pajot (1978). Skipjack tuna are quite commonly caught in traps and drive-in nets in the Philippines ([Philippines.] Bureau of Fisheries and Aquatic Resources 1980).

5.2 Fishing areas

The major fisheries have developed adjacent to continents or large islands where upwelling or other oceanographic features lead to a concentration of skipjack tuna near the surface (Fig. 10). The shaded areas around various islands have been exaggerated while subsistence fisheries in the South Pacific Ocean and the small but developing fishery off Australia have not been indicated. Generally, the surface fisheries extend from the neritic-pelagic environment into the adjacent, oceanic-pelagic environment. Reports of skipjack tuna being taken in estuarine environments (river plumes primarily) have been received from the southwestern Pacific Ocean. Open oceanic surface catches are generally associated with upwelling zones between opposing currents, such as along the equatorial currents, the Kuroshio, and the North Pacific subtropical countercurrent.

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[22] G. Habib, Forum Fisheries Agency, P.O. Box 627, Honiara, Solomon Islands, pers. commun. 26 June 1981.

[23] Petit, M. 1979. Compte-rendu succinct des travaux accomplis lors de la premiere, periode de l'operation radiometrie aerienene et prospection thoniere (06 fevrier 1979-11 avril 1979). Ref. Article 3 - paragraphe 3-2 du contract No. 1 DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, no pag. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[24] Petit, M. 1979. Compte-rendu des travaux accomplis lors de la deuxieme periode de l'operation radiometrie aerienne et prospection thoniere (16 juin 1979-14 juillet 1979). Ref. Article 3-2 du contract No. 1. DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, no pag. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[25] Petit, M., J. Muyard, and F. Marsac. 1980. Compte-rendu des travaux accomplis lors de la troisieme periode de l'operation radiometrie aerienne et prospection thoniere (25 septembre 1979-11 febvier 1980). Ref. Article 3-2 du contract No. 1. DOM-TOM-ORSTOM. O.R.S.T.O.M., Centre de Noumea, 77 p. O.R.S.T.O.M., B. P. A5, Noumea-Cedex, New Caledonia.

[26] Guillen, R., and D. A. Bratten. 1981. Anchored raft experiment to aggregate tunas in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Internal Rep. 14, 10 p. Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037.

5.3 Fishing seasons

Generally, fisheries existing in the equatorial, tropical areas do not show much seasonal variation except possibly a slight increase in catches during both the northern and southern summers. Fisheries situated more poleward in the subtropics or bordering on the temperate zone show more seasonality with the peak catches occurring in the summer months for the respective hemispheres.

Specific details on seasonality in various fisheries for the western Pacific and the Indian Oceans may be found in Uchida (1975), for New Zealand in Habib (1976, 1978) and Habib et al. (1980a, b, c), for Papua New Guinea in Wankowski (1980), for the eastern tropical Atlantic Ocean in Sakagawa and Murphy (1976), and for French Polynesia and the eastern tropical Pacific in Forsbergh (1980).

5.4 Fishing operations and results

5.41 Effort and intensity

Various means of measuring fishing effort directed at skipjack tuna were discussed in Section 4.2. Changes in the efficiency of the gear were discussed in Section 5.1.

In the eastern tropical Pacific, reported effort is 22 to 26% less than the total effort; however, there is no apparent trend in the rate of reporting (Forsbergh 1980). The amount of fishing effort increased from 1934 to the 1950's, remained fairly constant during the 1960's, and then increased again through most of the 1970's.

In Hawaii, estimates of relative fishing intensity (Fig. 70) fluctuated substantially from year to year and were at a somewhat higher level during the 1948-56 period than in subsequent years (Uchida 1976).

In the Papua New Guinea bait boat fishery, the amount of fishing effort has increased from some 500 d in 1970 to 8,000-9,000 d by 1979 (Wankowski 1980). In the New Zealand purse seine fishery, about 400 d of effort have been expended in each fishing season starting in 1976-77 (Habib 1976, 1978; Habib et al. 1980a, b).

For the Japanese bait boat fishery, there has been a slight increase in the number of trips from around 7,000 in 1970 to 10,000 in 1976 by all size classes of boats in the coastal fishery (north of lat. 15°N), while for boats between 50 and 100 gross metric tons (GMT), the number of trips increased from about 1,400 to 8,000 (Bour and Galenon 1979). For the southern water fishery, Kasahara (1977) showed that the total number of fishing days for all size classes of bait boats increased from nearly 9,000 in 1970 to over 21,000 in 1975, while the increase for 250 GMT boats was from around 2,600 to nearly 20,000 d during the same period. Honma and Suzuki (1978), in their preliminary description of the Japanese purse seine fishery, showed that the number of single-boat purse seiners increased from 16 in 1969 to 52 in 1974, whereas the number of double-boat purse seiners declined from 55 to 12 over the same period. The number of trips for the single-boat purse seiners varied from some 390 to 940 and for the double-boat purse seiners from 1,500 to about 340 over the same period. In the period 1971-74 the number of sets for single-boat seiners in the coastal fishery fluctuated between 1,000 and 2,000 sets, whereas for double-boat seiners the number of sets declined from around 1,300 to 400. In the southern water fishery, the number of sets by single-boat seiners increased from 60 in 1968 to 428 in 1974.

5.42 Selectivity

Pole-and-line gear (as used on bait boats) tends to take smaller and fewer size classes of skipjack tuna than does purse seine gear. The selectivity of pole-and-line gear can be modified by changing hook size, weight of the pole, or bait size, but most significantly by merely selecting for size of fish in a school. Likewise, the size selectivity of purse seine gear can be varied by selecting schools and by adjusting mesh size to retain fish only of the desired size or larger. Longline gear, which catches skipjack tuna only incidentally, is known to take mostly large individuals as discussed in Section 4.13.

5.43 Catches

(1) Total annual catches

From 1961 through 1979, the nominal catches of skipjack tuna from all oceans have more than tripled, reaching 698.5 t in 1979 (Table 19). While the catch of all tunas has increased varying amounts over this period, that for skipjack tuna has increased more rapidly than the other principal market species of tunas (yellowfin tuna, albacore, bigeye tuna, and bluefin tuna). More specifically, the proportion of skipjack tuna catches has increased steadily from 24.5% in 1961 to around 40% in the late 1970's (Fig. 76). Catches of skipjack tuna first surpassed those of the traditionally dominant yellowfin tuna in 1965, fell below in 1968 and 1969, and then remained above after 1970. Clearly the Pacific Ocean is the most important area for skipjack tuna fishing with catches there accounting for 80 to 90% of the world catch. Also, the fisheries of the western Pacific alone accounted for 67.1% of the world skipjack tuna catch in 1979 (Fig. 77). The developing fisheries in the Atlantic and the Indian Oceans accounted for 12.5 and 4.7% of the world skipjack tuna catch in 1979.

(2) Total annual yields from different fishing grounds

A more detailed breakdown of catches is provided in Table 20 for selected countries in the most productive skipjack tuna fishing areas. In the eastern central Atlantic Ocean, Spain and France have traditionally been the major producers but Japan, and more recently Korea, have become significant participants in the fishery. In the Indian Ocean, the production of the two major fishing countries, Maldives and Sri Lanka, has declined. In the northwestern Pacific Ocean, Japan is essentially the only producer, and their fishery reached a maximum of some 107,000 t in 1973. In the central western Pacific Ocean, the Japanese distant water fishery is the major producer and has shown a large increase from around 35,000 t in 1966 to 198,000 t in 1978. Production by the Philippines, Indonesia, Papua New Guinea, and the Solomons has also shown marked increases in the 1970's. In the eastern central Pacific Ocean, the United States has been the leading fishing nation, producing up to around 100,000 t. Ecuador has been the second largest producer, with a maximum of around 17,000 t. Mexico has recently been adding significantly to its purse seiner carrying capacity and should be expected to con-

Table 19.—Annual landings (in 1,000 t) of skipjack tuna from the major oceans by FAO statistical areas (FAO 1968, 1971, 1974b, 1976, 1977, 1978, 1979, 1980).

Area	Year																		
	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Atlantic Ocean[1]	0.3	0.3	2.2	14.3	17.9	25.7	22.7	36.2	32.0	51.6	67.9	73.1	71.8	119.0	67.8	73.5	97.6	95.6	87.6
Northwest 21	No breakdown by area			0.5	0.0	0.0	0.0	1.8	0.4	—	0.4	0.0	0.1	—	0.0	0.2	0.0	0.4	0.3
Northeast 27				—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.6
Western central 31				1.1	1.0	1.1	1.2	1.8	1.3	1.6	1.7	1.6	2.1	4.1	2.9	4.7	6.0	1.9	2.1
Eastern central 34				10.8	16.4	24.0	20.0	31.8	29.9	49.5	64.9	70.4	67.0	101.1	63.1	66.5	86.9	88.3	77.5
Southwest 41				0.4	0.5	0.6	1.5	0.8	0.4	0.4	0.8	1.0	0.6	0.5	1.1	0.6	0.6	1.4	1.4
Southeast 47				1.5	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	2.0	13.3	0.7	1.5	4.1	3.6	3.7
Indian Ocean	—	—	—	0	13.2	16.0	18.1	16.6	18.7	29.7	31.4	20.1	24.2	41.3	36.2	38.4	30.3	30.4	32.6
Western 51	No breakdown by area			0	13.2	16.0	18.1	16.5	18.6	27.4	29.0	16.3	20.1	36.7	31.7	32.4	26.2	25.3	27.0
Eastern 57				0	0.0	0.0	0.0	0.1	0.1	2.3	2.4	3.8	4.1	4.6	4.5	6.0	4.1	5.1	5.6
Pacific Ocean	219.0	252.4	200.8	252.4	235.9	308.6	335.9	273.6	269.6	304.0	328.2	330.1	434.3	510.0	436.3	554.3	504.8	665.8	578.3
Northwest 61	No breakdown by area			187.2	145.8	208.4	176.0	147.6	163.1	166.2	119.8	157.1	202.6	127.2	135.5	151.1	130.0	157.3	143.0
Northeast 67				—	0.2	—	0.1	—	0.1	0.2	0.3	0.0	0.1	0.5	0.1	6.7	0.4	5.8	0.5
Western central 71				—	—	35.7	35.2	42.5	41.5	70.0	114.8	119.9	173.0	303.0	205.4	252.9	272.5	359.7	316.9
Eastern central 77				53.4	76.3	54.2	106.9	74.5	51.5	58.9	87.4	50.1	52.0	75.3	84.5	134.2	91.4	130.0	107.7
Southwest 81				1.5	0.0	0.0	0.2	0.1	0.0	0.0	0.2	0.5	1.8	1.7	6.4	6.3	6.4	9.8	8.5
Southeast 87				10.3	13.6	10.3	17.5	8.9	13.4	8.7	5.7	2.5	4.8	2.3	4.4	3.1	4.1	3.2	1.7
Total	219.3	252.7	203.0	266.7	267.0	350.3	376.7	326.4	320.3	385.3	427.3	423.3	530.3	670.3	540.3	662.2	632.7	791.8	698.5

[1] Landings occur in the Mediterranean but in very small amounts.

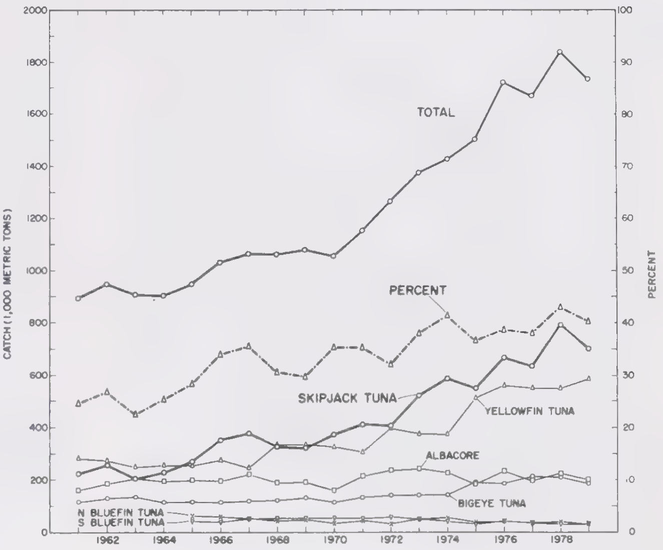

Figure 76.—Annual nominal catches of the principal market species of tunas from all oceans (FAO 1968, 1973, 1975, 1979, 1980) and catches of skipjack tuna as a percent of the total.

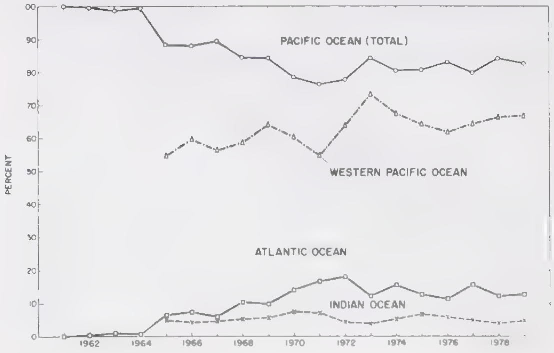

Figure 77.—Percent of skipjack tuna catches by ocean areas.

Table 20.—Annual landings (in 1,000 t) of skipjack tuna by states within key FAO statistical areas (FAO 1968, 1971, 1974b, 1976, 1977, 1978, 1979, 1980).

	Eastern central Atlantic Ocean - 34				Western Indian Ocean - 51		Northwestern Pacific Ocean - 61	Western central Pacific Ocean - 71					Eastern central Pacific Ocean - 77	
Year	Spain	France	Japan	Korea	Maldives	Sri Lanka	Japan	Japan	Philippines	Indonesia	Papua New Guinea	Solomon Islands	United States	Ecuador
1964	2.9	—	3.1	—	—	—	162.6	—	—	—	—	—	41.8	9.3
1965	9.5	—	6.3	—	13.1	—	132.8	—	—	—	—	—	58.1	14.9
1966	18.5	—	4.4	—	15.9	—	191.6	35.7	—	—	—	—	44.1	10.5
1967	13.6	—	3.7	—	17.9	—	154.2	34.7	0.5	—	—	—	93.6	17.3
1968	19.1	—	7.3	—	16.3	—	125.9	40.1	2.4	—	—	—	50.8	12.9
1969	18.3	—	4.9	—	18.4	—	138.8	40.9	0.6	—	—	—	35.1	15.6
1970	22.2	10.6	7.5	—	27.3	—	151.3	53.4	0.3	12.1	2.4	—	39.3	8.8
1971	27.1	9.7	11.7	0.0	28.9	—	99.1	79.3	0.6	12.4	17.0	4.5	77.3	11.9
1972	22.5	15.2	10.2	0.0	16.0	—	156.2	79.7	0.3	19.6	13.1	6.8	22.1	4.5
1973	22.1	12.7	13.1	0.9	20.0	—	200.9	106.9	3.2	22.3	28.5	5.8	27.3	4.4
1974	36.5	18.4	18.7	2.2	24.0	12.3	125.6	196.2	29.5	23.6	40.2	10.0	48.5	7.8
1975	17.8	10.4	3.6	4.7	16.0	15.2	133.3	119.5	31.7	23.3	15.6	7.1	66.2	17.0
1976	18.5	15.5	13.2	1.9	19.9	12.2	149.2	145.3	29.2	25.3	24.4	15.6	87.7	6.2
1977	19.6	24.9	13.2	4.2	14.4	11.4	126.8	148.8	55.1	26.4	19.2	13.0	51.2	10.0
1978	28.9	19.2	14.6	7.4	13.8	11.0	152.3	198.3	49.7	29.4	45.8	17.5	100.5	11.8
1979	19.8	14.7	12.4	12.0	17.9	8.3	139.4	177.4	45.1	30.2	24.0	23.8	72.5	17.6

tribute proportionally more to the total production from the area.

6 PROTECTION AND MANAGEMENT

As yet there are no management regulations for skipjack tuna in any of the world's oceans. From a biological viewpoint, no need for conservation measures has been proven for any fishery, although Kasahara (1977) and others have cautioned that expansion of the fisheries should be done with a knowledge of the limits of the available resources. Kearney (1978, 1979) believed that attempts to optimize socioeconomic returns among participants in the fisheries and states controlling fishing in their extended economic zones will overshadow any conservation needs for many years to come.

As many nations around the world have declared extended economic zones and have begun to regulate fishing activities in their zones, de facto regulation is, in fact, occurring now. However, the goal of the nations promulgating these regulations is to extract economic returns from foreigners fishing in their respective zones or to reserve the resources for domestic harvest. As yet these regulatory measures have been declared unilaterally with no multilateral or international arrangements being effected. Various states in the eastern tropical Pacific, South Pacific, western Pacific, and Indian Oceans are moving toward such international arrangements, but none have been completed.

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Myctophidae: Development

H. G. Moser, E. H. Ahlstrom and J. R. Paxton

LANTERNFISHES of the family Myctophidae are found in all oceans of the world. Some 230–250 species are arranged in 36 generic/subgeneric taxa (Table 59). All nominal species are listed in Paxton (1979). Characteristic of the family is the presence of light organs or photophores on the head and body (Fig. 114). The different patterns of photophores have been used, along with meristics (Table 60), in species diagnoses and as a basis for classification within the family since the late 1800's.

Most authors have placed the Myctophidae and closely related Neoscopelidae with the families Aulopidae, Chlorophthalmidae and related families in an order or suborder variously named the Iniomi, Myctophoidea or Myctophiformes (Gosline et al., 1966; Greenwood et al., 1966; Nelson, 1976; Johnson, 1982), although Rosen (1973) separated the Myctophidae and Neoscopelidae as a restricted order Myctophiformes. Moser and Ahlstrom (1970, 1972, 1974), Ahlstrom et al. (1976) and Paxton (1972) are the most recent papers considering relationships within the family; characteristics of larvae and bones and photophores of adults were primarily utilized in the respective studies. Paxton's (1972) classification, including genera recognized subsequently, is as follows:

- Subfamily Myctophinae
  - Tribe Electronini
    - Genera: *Protomyctophum, Krefftichthys*[1], *Electrona, Metelectrona*[2]
  - Tribe Myctophini
    - Genera: *Benthosema, Diogenichthys, Hygophum, Myctophum, Symbolophorus*
  - Tribe Gonichthyini
    - Genera: *Loweina, Tarletonbeania, Gonichthys, Centrobranchus*
- Subfamily Lampanyctinae
  - Tribe Notolychnini
    - Genus *Notolychnus*
  - Tribe Lampanyctini
    - Genera: *Taaningichthys, Lampadena, Bolinichthys, Lepidophanes, Ceratoscopelus, Stenobrachius, Lampanyctus, Triphoturus, Parvilux*[3]
  - Tribe Diaphini
    - Genera: *Lobianchia, Diaphus, Idiolychnus*[4]
  - Tribe Gymnoscopelini
    - Genera: *Lampanyctodes, Gymnoscopelus, Notoscopelus, Lampichthys, Scopelopsis, Hintonia*

There has not been a family revision at the species level since Fraser-Brunner's (1949) study. A large number of more recent generic revisions and regional studies are currently the primary sources for species identifications; most of these have been utilized in compiling the generic distribution limits (Table 59). The most recent zoogeographic studies are those of Backus et al.

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[1] Hulley (1981).

[2] Wisner (1963).

[3] Hubbs and Wisner (1964).

[4] Nafpaktitus and Paxton (1978).

TABLE 59. GEOGRAPHIC DISTRIBUTION OF THE GENERA AND SUBGENERA OF MYCTOPHIDAE. References marked * are useful for the identification of species. The division of the Atlantic and Indian Oceans is arbitrarily taken at 20°E, the Indian-Pacific Ocean boundary at 130°E.

Genus	No. of species	Ocean	Lat. extremes	References
Krefftichthys	1	Atlantic	34°S–60°S	*Hulley (1981:12)
		Indian	43°S–66°S	*Hulley (1972:217); Andriashev (1962:224)
		Pacific	34°S–72°S	Andriashev (1962:225); McGinnis (1982:11)
Protomyctophum (*Protomyctophum*)	7	Atlantic	34°S–60°S	*Hulley (1981:29, 19)
		Indian	44°S–65°S	Hulley (1972:218); *McGinnis (1982:17)
		Pacific	40°S–70°S	*Andriashev (1962); *McGinnis (1982:16, 17)
Protomyctophum (*Hierops*)	7	Atlantic	70°N–56°S	Nafpaktitis et al. (1977:31); *Hulley (1981:36)
		Indian	35°S–52°S	*Nafpaktitis and Nafpaktitis (1969:7); *McGinnis (1982:18)
		Pacific	57°N–67°S	*Wisner (1976:20); *McGinnis (1982:18)
Electrona	5	Atlantic	55°N–70°S	*Hulley (1981:40, 46); *McGinnis (1982:21)
		Indian	2°N–68°S	Nafpaktitis and Nafpaktitis (1969:10); *McGinnis (1982:21)
		Pacific	42°N–70°S	*Andriashev (1962); Ebeling (1962:140); *McGinnis (1982:21)
Metelectrona	2	Atlantic	35°S–51°S	*Hulley (1981:53)
		Indian	35°S–47°S	*McGinnis (1982:25)
		Pacific	33°S–55°S	*Bussing (1965:200); *McGinnis (1982:25)
Benthosema	5	Atlantic	80°N–38°S	*Nafpaktitis et al. (1977:52); Hulley (1972:220); (the specimen from 55°S is possibly mislabeled, McGinnis, (1982:26, 29))
		Indian	21°N–35°S	Kotthaus (1972:18); *Nafpaktitis and Nafpaktitis (1969:11)
		Pacific	71°N–42°S	*Wisner (1976); Nafpaktitis et al. (1977:52); Robertson et al. (1978:302)
Diogenichthys	3	Atlantic	50°N–48°S	Nafpaktitis et al. (1977:58); Hulley (1981:58)
		Indian	18°N–45°S	*Nafpaktitis and Nafpaktitis (1969:15)
		Pacific	37°N–41°S	*Wisner (1976:49); Rass (1960:149)
Hygophum	9–11	Atlantic	49°N–48°S	*Bekker (1965); *Nafpaktitis et al. (1977:38); *Hulley (1981:61)
		Indian	20°N–42°S	*Bekker (1965:80); Hulley (1972:222)
		Pacific	39°N–46°S	*Wisner (1976); *Bekker (1965:94); McGinnis (1982:30)
Symbolophorus	7–9	Atlantic	59°N–51°S	*Hulley (1981:101)
		Indian	21°N–41°S	Kotthaus (1972:27); *Nafpaktitis and Nafpaktitis (1969:29)
		Pacific	50°N–59°S	*Wisner (1976); Frost and McCrone (1979:755); *McGinnis (1982:33)
Myctophum	13–14	Atlantic	65°N–40°S	*Nafpaktitis et al. (1977:62); *Hulley (1981:87)
		Indian	20°N–34°S	Nafpaktitis and Nafpaktitis (1969); *Bekker and Borodulina (1978:120); McGinnis (1982:34)
		Pacific	42°N–42°S	*Kawaguchi and Aioi (1972); *Wisner (1976); Kawaguchi et al. (1972:27); Paxton and Nafpaktitis (ms)
Loweina	3–4	Atlantic	44°N–38°S	*Nafpaktitis et al. (1977:85)
		Indian	10°S–40°S	*Bekker (1964:23); *Nafpaktitis and Nafpaktitis (1969:31)
		Pacific	32°N–40°S	*Wisner (1976); *Bekker (1964:23); McGinnis (1982:37)
Tarletonbeania	1–2	Atlantic	—	
		Indian	—	
		Pacific	50°N–30°N	*Bekker (1963:160); *Wisner (1976:82)
Gonichthys	3–4	Atlantic	47°N–40°S	Nafpaktitis et al. (1977:88); Hulley (1981:107)
		Indian	25°S–39°S	*Bekker (1964:38)
		Pacific	31°N–42°S	*Bekker (1964); *Wisner (1976:86); McGinnis (1982:36)
Centrobranchus	3–4	Atlantic	46°N–35°S	*Nafpaktitis et al. (1977:91)
		Indian	15°N–33°S	*Bekker (1964:51, 58)
		Pacific	37°N–37°S	*Bekker (1964:58)
Notolychnus	1	Atlantic	56°N–38°S	*Nafpaktitis et al. (1977:94); *Hulley (1972:222)
		Indian	11°N–40°S	Kotthaus (1972:30); McGinnis (1982:37)
		Pacific	34°N–44°S	Ebeling (1962:141); McGinnis (1982:37)
Lobianchia	2	Atlantic	61°N–51°S	*Nafpaktitis et al. (1977); Bekker (1967:98); McGinnis (1982:51)
		Indian	2°N–40°S	*Nafpaktitis (1978:7); McGinnis (1982:51)
		Pacific	32°N–47°S	*Wisner (1976:96); McGinnis (1982:51)
Diaphus	65–75	Atlantic	62°N–52°S	*Nafpaktitis et al. (1977:158); McGinnis (1982:52)
		Indian	23°N–48°S	*Nafpaktitis (1978:62, 78)
		Pacific	55°N–58°S	*Nafpaktitis (1978:62); McGinnis (1982:52)
Idiolychnus	1	Atlantic	—	
		Indian	13°S–24°S	*Nafpaktitis and Paxton (1978:495)
		Pacific	21°N	*Nafpaktitis and Paxton (1978:495–496)

TABLE 59. CONTINUED.

Genus	No. of species	Ocean	Lat. extremes	References
Lampanyctodes	1	Atlantic	19°S–34°S	*Ahlstrom et al. (1976:146); Grindley and Penrith (1965:283)
		Indian	35°S	Paxton and Nafpaktitis (in prep.)
		Pacific	34°S–51°S	*Wisner (1976:158–159); McGinnis (1982:55)
Gymnoscopelus (*Gymnoscopelus*)	4	Atlantic	34°S–66°S	*Hulley (1981:254); *McGinnis (1982:59)
		Indian	60°S–65°S	*Andriashev (1962:267); *McGinnis (1982:59)
		Pacific	40°S–72°S	*McGinnis (1982:61, 58)
Gymnoscopelus (*Nasolychnus*)	4–5	Atlantic	34°S–57°S	*Hulley (1981:261); (03°S, Fraser-Brunner (1931:224) presumably a waif)
		Indian	24°S–65°S	Smith (1933a:126); *McGinnis (1982:64)
		Pacific	40°S–70°S	*Andriashev (1962); McGinnis (1982:64)
Scopelopsis	1	Atlantic	11°S–48°S	*Hulley (1981:241)
		Indian	9°S–40°S	Legand (1967:49); McGinnis (1982:57)
		Pacific	15°S–35°S	*Wisner (1976:222); Paxton and Nafpaktitis (in prep.)
Lampichthys	1	Atlantic	30°S–48°S	Hulley (1981:242)
		Indian	35°S–40°S	McGinnis (1982:57)
		Pacific	7°S–49°S	*Wisner (1976:215); McGinnis (1982:57)
Notoscopelus (*Notoscopelus*)	5	Atlantic	65°N–60°S	*Nafpaktitis et al. (1977:254) Andriashev (1962:278)
		Indian	8°S–36°S	Nafpaktitis and Nafpaktitis (1969:35); Grindley and Penrith (1965:283)
		Pacific	50°N–37°S	*Fujkii and Uyeno (1976); Frost and McCrone (1979:755); Collins and Baron (1981:11)
Notoscopelus (*Parieophus*)	1	Atlantic	50°N–21°N	*Nafpaktitis et al. (1977:257)
		Indian	—	
		Pacific	—	
Hintonia	1	Atlantic	39°S–48°S	*Hulley (1981:239)
		Indian	47°S–51°S	McGinnis (1982:55)
		Pacific	40°S–50°S	*Wisner (1976:220); McGinnis (1982:55)
Lampadena (*Lampadena*)	8–9	Atlantic	65°N–48°S	*Krefft (1970:285); Hulley (1981:180)
		Indian	6°N–49°S	*Nafpaktitis and Paxton (1968:20, 21)
		Pacific	41°N–49°S	*Nafpaktitis and Paxton (1968:20, 21)
Lampadena (*Dorsadena*)	1	Atlantic	—	
		Indian	—	
		Pacific	45°N	*Coleman and Nafpaktitis (1972:2)
Taaningichthys	3	Atlantic	43°N–44°S	*Hulley (1981:167); *Davy (1972)
		Indian	8°N–30°S	*Nafpaktitis and Nafpaktitis (1969:40)
		Pacific	41°N–68°S	*Davy (1972:72); *Nafpaktitis et al. (1977:191)
Ceratoscopelus	3	Atlantic	52°N–45°S	*Nafpaktitis et al. (1977:243); Hulley (1981:237)
		Indian	20°N–43°S	*Bekker and Borodulina (1968:792); *Nafpaktitis and Nafpaktitis (1969:65)
		Pacific	43°N–42°S	*Wisner (1976:207); Robertson et al. (1978:302)
Lepidophanes	2	Atlantic	43°N–48°S	*Nafpaktitis et al. (1977:225); *Hulley (1981:223)
		Indian	—	
		Pacific	—	
Bolinichthys	7	Atlantic	53°N–41°S	*Nafpaktitis et al. (1977:240); *Hulley (1981:229)
		Indian	21°N–44°S	Kotthaus (1972:18); *Nafpaktitis and Nafpaktitis (1969:60)
		Pacific	31°N–43°S	*Johnson (1975:58); Nafpaktitis et al. (1977:234)
Triphoturus	3–4	Atlantic	—	Hulley (1981:205)
		Indian	8°N–14°S	*Nafpaktitis and Nafpaktitis (1969:51)
		Pacific	38°N–35°S	*Wisner (1976:165)
Stenobrachius	2	Atlantic	—	
		Indian	—	
		Pacific	57°N–30°N	*Wisner (1976:160)
Parvilux	2	Atlantic	—	
		Indian	—	
		Pacific	40°N–14°S	*Wisner (1976:163, 164)
Lampanyctus	40	Atlantic	65°N–60°S	*Nafpaktitis et al. (1977:196); *Hulley (1981:183); Zahuranec (1980)
		Indian	16°N–60°S	*Nafpaktitis and Nafpaktitis (1969); Kotthaus (1972:35); *McGinnis (1982:42); Zahuranec (1980)
		Pacific	59°N–72°S	*Wisner (1976:191); McGinnis (1982:42); Zahuranec (1980)

TABLE 60. MERISTICS OF THE GENERA AND SUBGENERA OF MYCTOPHIDAE.

	Fin rays							
	Dorsal	Anal	Pectoral	Pelvic	Procurrent caudal	Vertebrae	Branchiostegals	Gill rakers
Krefftichthys	11–14	17–19	14–16	8–9	8–9 + 7–9	36–39		6–8 + 19–23
Protomyctomphum	10–14	21*–27	14–17	8–9	7–9 + 6–9	35–41	8–10	4–7 + 14–21
P. Hierops	11–13	20–27	15–18	8	7–11 + 6–9	36–42	9–10	3–5 + 13–18
Electrona	12–16	18–22	11–17	8	6–10 + 6–9	33–41	7–8	3–10 + 12–25
Metelectrona	13–15	19–22	14–16	8	10 + 9	35–38	8	4–7 + 16–20
Benthosema	11–15	16–22	10–17	8–9	7–9 + 7–9	31–37	9	3–10 + 10–21
Diogenichthys	10–13	14–18	10–14	7–8	7–9 + 7–9	29–34	7	2–4 + 10–12
Hygophum	10–15	18–25	12–17	8–9	6–9 + 6–9	34–40	9	3–6 + 12–16
Myctophum	11–15	16–27	12–22	7–8	7–9 + 7–9	35–46	8–9	4–8 + 10–21
Symbolophorus	12–16	18–24	12–20	8	8–10 + 7–9	36–42	9	4–7 + 12–19
Loweina	10–13	13–17	9–12	7–9	6–7 + 6–7	37–39	9	2–3 + 5–10
Tarletonbeania	11–15	16–20	11–16	8	5–8 + 5–8	40–42	8	4–6 + 10–12
Gonichthys	10–13	17–24	11–18	6–8	5–6 + 5–6	38–41	9	3–6 + 7–12
Centrobranchus	9–12	16–20	11–17	8	5–7 + 5–7	35–40	7–8	0
Notolychnus	10–12	12–15	11–15	6–7	7–9 + 7–9	27–31	9–10	2 + 8–9
Lobianchia	15–18	13–15	11–15	8	5–7 + 5–6	33–35	9	4–6 + 11–16
Diaphus	10–19	11–19	9–14	8	5–8 + 5–8	31–37	8–9	4–11 + 9–21
Idiolychnus	14–15	14–16	13–15	8		34		6–7 + 14–15
Lampanyctodes	13–14	14–17	12–14	8	8–10 + 9–10	36–39	9–11	10–11 + 20–23
Gymnoscopelus	14–21	16–22	12–16	8–9	10–12 + 11–15	41–45	10	6–12 + 14–26
G. Nasolychnus	16–20	16–20	12–15	8	8–13 + 10–15	41–45	10–11	7–12 + 17–25
Scopelopsis	20–24	23–27	10–12	7–8	9–11 + 11–12	38–39	9–10	7–9 + 16–18
Lampichthys	16–18	21–23	11–15	8	10 + 12	40–41	9	4–6 + 13–16
Notoscopelus	21–27	18–21	11–14	8–9	10–14 + 10–15	35–40	10	4–10 + 9–22
N. Parieophus	23–26	18–20	12–14			37–38		8–10 + 18–20
Hintonia	14–16	12–14	13–15	8	10–11 + 13	37–39	9	6–7 + 11–14
Lampadena	13–16	12–15	13–18	8	8 + 8–9	35–40	9	3–8 + 9–18
L. Dorsadena	14–15	12–14	15–16	8–9				4–5 + 12
Taaningichthys	11–14	11–14	12–17	8	7–10 + 6–10	34–41	8–9	2–5 + 6–14
Ceratoscopelus	13–15	13–16	12–15	8	6–7 + 6–7	35–38	9	3–5 + 9–16
Lepidophanes	11–15	13–16	11–14	8–9	6–7 + 6–8	33–37	9	3–4 + 8–11
Bolinichthys	11–15	11–15	11–15	8	7 + 7–8	33–36	9	3–7 + 11–17
Triphoturus	12–16	13–18	8–10	8	5–7 + 6–7	30–36	10–11	2–4 + 8–11
Stenobrachius	12–15	14–16	8–10	8	6–8 + 7–9	35–38	9–10	5–6 + 12–14
Parvilux	14–17	15–18	10–13	8	8 + 8–9	35–38	10–11	4–6 + 11–15
Lampanyctus	10–19	14–21	0–17	8	6–8 + 6–8	30–40	8–11	3–8 + 9–19

* Incorrectly 15–27 in Paxton, 1972.

(1977) and Hulley (1981) on Atlantic species and McGinnis (1982) on Southern Ocean species.

Most lanternfishes make extensive vertical migrations from mesopelagic depths to the upper waters at night, some reaching the surface (Paxton, 1967). The fisheries potential of myctophids and other mesopelagic fishes has recently been reviewed (Gjøsaeter and Kawaguchi, 1980). Adults range in size from 20–300 mm (Krefft, 1974) and have a life span of from one year in some tropical species (Clarke, 1973) to more than five years in the few temperate species that have been studied (Smoker and Pearcy, 1970; Gjøsaeter, 1973; Kawaguchi and Mauchline, 1982).

EGGS

Myctophids are oviparous and presumably all produce planktonic eggs although such have been reported for only two species. Sanzo (1939a) indicated that mature ovarian eggs of *E. rissoi* have the following characteristics: round shape; 0.80–0.84 mm diameter; segmented yolk; single oil globule, ca. 0.28 mm diameter; smooth chorion. He illustrated a planktonic egg with similar characteristics and tentatively identified it as that of *E. rissoi.* Robertson (1977) described the planktonic egg of *Lampanyctodes hectoris* as follows: weakly oval; long axis 0.74–0.83 mm, short axis 0.65–0.72 mm; strongly segmented yolk; single oil droplet, 0.21–0.23 mm diameter; narrow perivitelline space; chorion smooth and delicate. He based his identification on the similarity of these eggs and mature ovarian eggs of running ripe *L. hectoris* captured at the same time by trawl.

We have observed planktonic eggs similar to those described by Robertson (1977) but have not found them with advanced embryos that could be matched with co-occurring yolk-sac myctophid larvae. The fact that these and other types of eggs tentatively identified as myctophids occur in relatively low abundance compared with myctophid larvae led Moser and Ahlstrom (1970) to suggest that the fragile chorion breaks in contact with plankton nets and the embryo is extruded through the mesh.

LARVAE

Moser and Ahlstrom (1970) reviewed the literature on myctophid larvae; however, numerous recent contributions have advanced our knowledge of the group and are listed in Table 61. Of the 32 recognized genera of myctophids, larvae have been described for all but *Hintonia.* The larval stages of myctophids provide sets of characters that are useful at levels of systematic analysis from species separation to hypotheses of

TABLE 61. SUMMARY OF LITERATURE CONTAINING ILLUSTRATIONS OF DEVELOPMENTAL STAGES OF MYCTOPHIDS. Frequently cited authors are abbreviated as follows: Ahlstrom (A), Belyanina and Kovalevskaya (B + K), Dekhnik and Sinyukova (D + S), Moser and Ahlstrom (M + A), Pertseva-Ostroumova (P-O), Shiganova (S), Tåning (T).

Species	Single larval stage	Multiple larval stages	Transforming stage	Juvenile stage
Benthosema				
fibulatum	M + A, 1974	P-O, 1974	—	—
glaciale	Holt, 1898; S, 1977	T, 1918; Sparta, 1951; M + A, 1974	Holt, 1898; T, 1918; Sparta, 1951	Holt, 1898; T, 1918; Sparta, 1951
panamense	—	M + A, 1970	M + A, 1970	M + A, 1970
pterota	M + A, 1974; P-O, 1974	Tsokur, 1981	—	Tsokur, 1981
suborbitale	P-O, 1964; M + A, 1974	P-O, 1974; Badcock and Merrett, 1976; S, 1977	P-O, 1974; S, 1977	S, 1977
Bolinichthys				
distofax	M + A, 1974	—	—	—
pyrsobolus	P-O, 1964	—	—	—
Centrobranchus				
andrae	P-O, 1974	—	P-O, 1974	—
brevirostris	P-O, 1964	P-O, 1974	—	—
choerocephalus	M + A, 1974	M + A, 1970	—	M + A, 1970
nigroocellatus	P-O, 1974	—	—	—
Ceratoscopelus				
maderensis	M + A, 1972; S, 1977	T, 1918; D + S, 1966	T, 1918	T, 1918; S, 1977
townsendi	M + A, 1974	—	—	—
warmingi	Miller et al., 1979; Belyanina, 1982b	S, 1977	S, 1977	—
Diaphus				
agassizii	—	P-O, 1975	P-O, 1975	P-O, 1975
holti	D + S, 1966	T, 1918	T, 1918	T, 1918
malayanus	—	Tsokur, 1975	Tsokur, 1975	Tsokur, 1975
metapoclampus	—	Sparta, 1952	Sparta, 1952	Sparta, 1952
mollis	—	S, 1977	S, 1977	S, 1977
pacificus	M + A, 1974	—	—	—
rafinesquei	—	T, 1918	T, 1918	T, 1918
theta	P-O, 1964; M + A, 1974	—	—	—
Diogenichthys				
atlanticus	P-O, 1964	T, 1918; A, 1965; M + A, 1970; P-O, 1974; S, 1977	T, 1918; M + A, 1970; S, 1977	T, 1918; M + A, 1970; S, 1977
laternatus	—	A, 1965; M + A, 1970	M + A, 1970	M + A, 1970
panurgus	—	P-O, 1974	P-O, 1974	—
Electrona				
antarctica	M + A, 1974	P-O, 1967; B + K, 1979	—	—
carlsbergi	M + A, 1974	B + K, 1979	—	—
rissoi	—	T, 1918; Sanzo, 1939a; D + S, 1966; M + A, 1970	Sanzo, 1939a	T, 1918; Sanzo, 1939a; M + A, 1970
subaspera	M + A, 1974	—	—	—
Gonichthys				
coccoi	—	T, 1918; S, 1977; D + S, 1966	—	T, 1918; S, 1977
tenuiculus	M + A, 1974	M + A, 1970	M + A, 1970	—
Gymnoscopelus				
bolini	—	S, 1977	S, 1977	S, 1977
braueri	P-O, 1964	P-O, 1977; B + K, 1979	—	—
fraseri	—	P-O, 1977	—	—
nicholsi	P-O, 1964	M + A, 1972; P-O, 1977; B + K, 1979	M + A, 1972	—
opisthopterus	—	Yefremenko, 1977	—	—
Hygophum				
atratum	—	M + A, 1970	M + A, 1970	M + A, 1970
benoiti	—	T, 1918; S, 1974	T, 1918; S, 1974	T, 1918; S, 1974
brunni	M + A, 1974	—	—	—
hanseni	—	S, 1977	S, 1977	S, 1977
hygomi	M + A, 1974	T, 1918; P-O, 1974; S, 1977	T, 1918; P-O, 1974; S, 1977	T, 1918; S, 1977

TABLE 61. CONTINUED.

Species	Single larval stage	Multiple larval stages	Transforming stage	Juvenile stage
macrochir	M + A, 1974	S, 1975	S, 1975	S, 1975
proximum	M + A, 1974; Miller et al., 1979	P-O, 1974	P-O, 1974	—
reinhardti	M + A, 1974	M + A, 1970; S, 1977	M + A, 1970; S, 1977	M + A, 1970; S, 1977
taaningi	M + A, 1974	—	—	—
Idiolychnus				
urolampus	M + A, 1974	—	—	—
Krefftichthys				
anderssoni	M + A, 1974	Yefremenko, 1976; B + K, 1979	Yefremenko, 1976	Yefremenko, 1976
Lampadena				
luminosa	M + A, 1974; Miller et al., 1979	—	—	—
urophaos	—	M + A, 1972	M + A, 1972	—
Lampanyctodes				
hectoris	—	Ahlstrom et al., 1976	Ahlstrom et al., 1976	Ahlstrom et al., 1976
Lampanyctus				
achirus	M + A, 1974	—	—	—
crocodilus	—	T, 1918; D + S, 1966	T, 1918	T, 1918
jordani	P-O, 1964	—	—	—
nobilis	Miller et al., 1979	—	—	—
pusillus	—	T, 1918; D + S, 1966	T, 1918	T, 1918
regalis	M + A, 1974	—	Bolin, 1939b	—
ritteri	M + A, 1974	A, 1965	—	—
Lampichthys				
procerus	—	M + A, 1972	M + A, 1972	—
Lepidophanes				
gaussi	M + A, 1974	—	—	—
guentheri	M + A, 1972	S, 1977	M + A, 1972; S, 1977	—
Lobianchia				
dofleini	M + A, 1974	T, 1918; D + S, 1966; S, 1977	T, 1918; S, 1977	T, 1918; S, 1977
gemellari	Sanzo, 1931c; P-O, 1964; M + A, 1974	T, 1918	T, 1918	T, 1918
Loweina				
rara	M + A, 1974	M + A, 1970; P-O, 1974	M + A, 1970	M + A, 1970
terminata	Belyanina, 1982b	—	—	—
Metelectrona				
ventralis	M + A, 1974	—	—	—
Myctophum				
asperum	P-O, 1964; M + A, 1974	Imai, 1958; P-O, 1974	—	Imai, 1958; P-O, 1974
aurolaternatum	M + A, 1974	—	—	—
brachygnathum	M + A, 1974	—	—	—
lychnobium	M + A, 1974; P-O, 1974	—	P-O, 1974	—
nitidulum	M + A, 1974	M + A, 1970; P-O, 1974	—	M + A, 1970
obtusirostre	M + A, 1974	—	—	—
punctatum	M + A, 1974	Sanzo, 1915b; T, 1918; S, 1977	Sanzo, 1915b; T, 1918; S, 1977	T, 1918; S, 1977
selenops	M + A, 1974	—	—	—
spinosum	M + A, 1974	P-O, 1974	P-O, 1974	P-O, 1974
Notolychnus				
valdiviae	P-O, 1964; M + A, 1974	T, 1918	T, 1918	T, 1918
Notoscopelus				
caudispinosus	Belyanina, 1982b	—	—	—
elongatus	—	T, 1918	T, 1918	T, 1918
resplendens	M + A, 1974	M + A, 1972; Badcock and Merrett, 1976; S, 1977	M + A, 1972; S, 1977	—

TABLE 61. CONTINUED.

Species	Single larval stage	Multiple larval stages	Transforming stage	Juvenile stage
Parvilux				
ingens	M + A, 1974	—	—	—
Protomyctophum				
arcticum	—	T, 1918	T, 1918	T, 1918
bolini	—	P-O, 1967; B + K, 1979	—	—
chilensis	M + A, 1974	—	—	—
crockeri	—	M + A, 1970	—	M + A, 1970
normani	P-O, 1967; M + A, 1974	—	—	P-O, 1967
parallelum	—	P-O, 1967; B + K, 1979	—	—
subparallelum	M + A, 1974	—	—	—
tenisoni	M + A, 1974	—	—	—
thompsoni	P-O, 1964	P-O, 1967; M + A, 1970	—	M + A, 1970
Scopelopsis				
multipunctatus	—	M + A, 1972; P-O, 1972	M + A, 1972; P-O, 1972; M + A, 1974	M + A, 1972
Stenobrachius				
leucopsarus	P-O, 1964; M + A, 1974	Fast, 1960; A, 1965; A, 1972b	Fast, 1960	Fast, 1960
Symbolophours				
boops	—	P-O, 1974	—	—
californiense	P-O, 1964; M + A, 1974	A, 1965; M + A, 1970; P-O, 1974	M + A, 1970; P-O, 1974	—
evermanni	P-O, 1964	P-O, 1974	P-O, 1974	P-O, 1974
veranyi	—	Sanzo, 1915b; T, 1918; D + S, 1966	Sanzo, 1915b; T, 1918	Sanzo, 1915b, T, 1918
Taaningichthys				
minimus	—	M + A, 1972	—	—
Tarletonbeania				
crenularis	P-O, 1964; M + A, 1974; P-O, 1974	A, 1965; M + A, 1970	Bolin, 1939b; M + A, 1970	M + A, 1970
Triphoturus				
mexicanus	M + A, 1974	A, 1965; A, 1972b	—	—
nigrescens	Moser, 1981	—	—	—

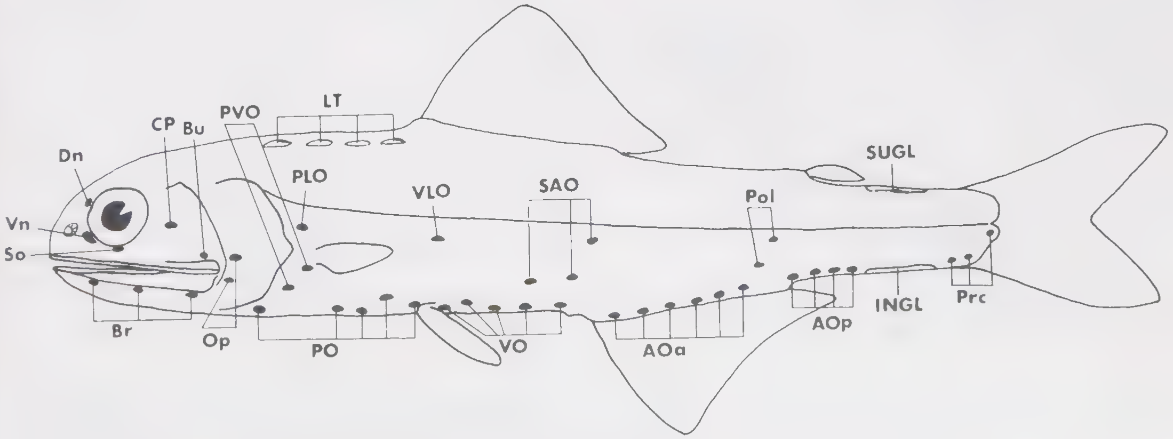

Fig. 114. Hypothetical myctophid showing photophore terminology, from Paxton (1972).

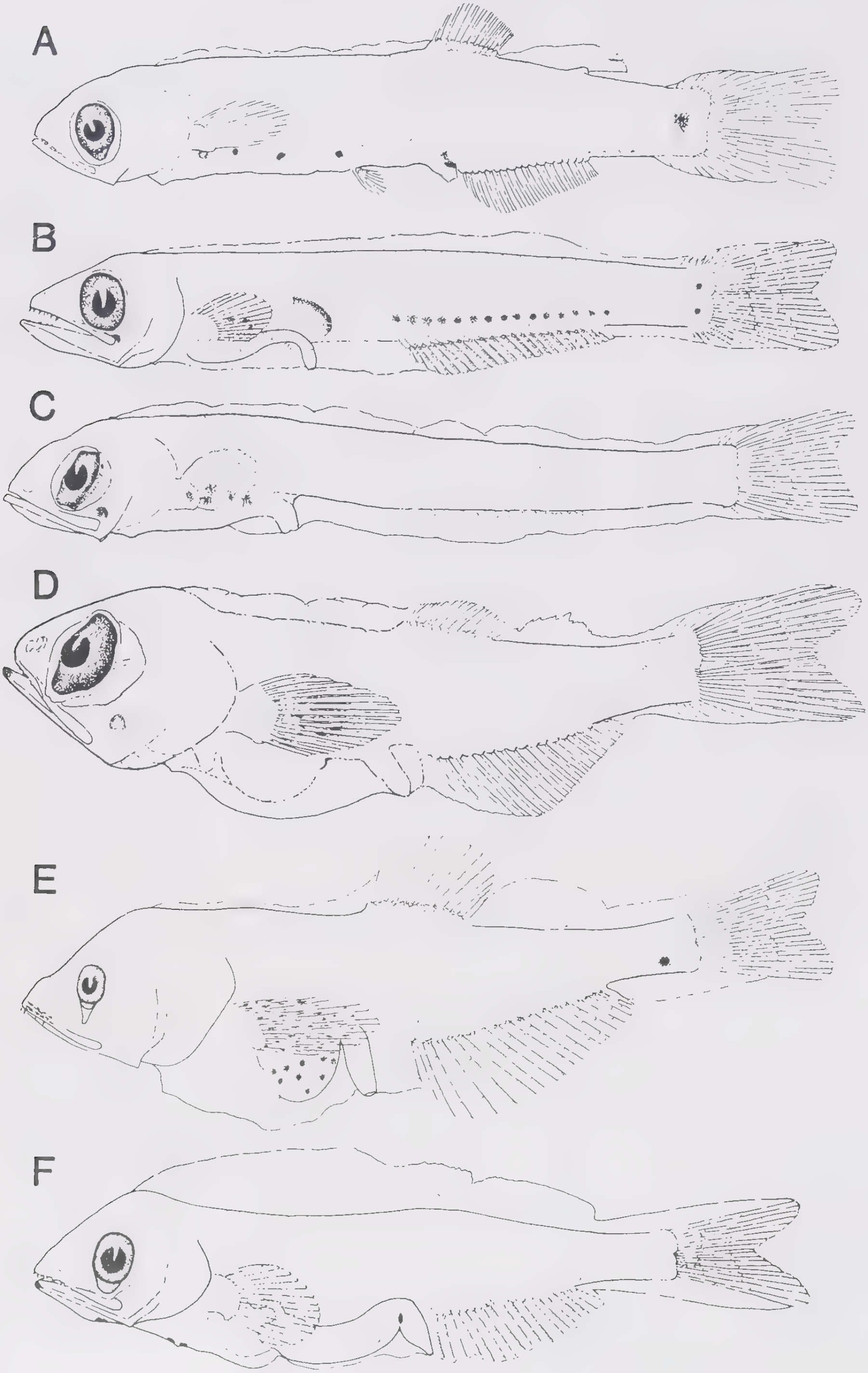

Fig. 115. Larvae of Electronini. (A) *Krefftichthys anderssoni*, 15.7 mm; (B) *Protomyctophum normani*, 15.2 mm; (C) *P. Heirops thompsoni*, 13.8 mm; (D) *Electrona rissoi*, 7.9 mm; (E) *E. antarctica*, 12.7 mm; (F) *Metelectrona ventralis*, 10.3 mm. A, B, E, F from Moser and Ahlstrom (1974); C and D from Moser and Ahlstrom (1970).

TABLE 62. SEQUENCE OF FORMATION OF PHOTOPHORES WHICH APPEAR IN FOURTEEN GENERA OF MYCTOPHIDAE. The Br_2 appear first in all genera listed. Parentheses indicate photophores appear late in larval period.

	Br_1	Br_3	Dn	Vn	OP_2	PO_1	PO_2	PO_3	PO_4	PO_5	PVO_1	PVO_2	PLO	VLO	VO_1	VO_5	AOa_1	AOa_2
Benthosema																		
suborbitale	2	2	—	—	2	1	1	3	3	3	—	—	—	—	—	—	3	3
glaciale	—	—	—	—	(1)	(1)	(1)	(1)	(1)	(1)	—	—	—	—	—	—	—	—
pterota	—	—	1	—	4	6	—	—	—	2	3	5	—	—	5	—	6	—
fibulatum	—	—	1	—	—	3	5	—	—	2	—	—	—	6	—	—	4	6
Diogenichthys																		
laternatus	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
atlanticus	—	—	—	—	—	—	1	—	—	2	—	—	—	—	—	—	3	—
Myctophum																		
spinosum	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
lychnobium	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
asperum	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
brachygnathum	—	—	1	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—
obtusirostre	—	—	1	—	—	3	—	—	—	—	—	—	2	—	—	—	—	—
selenops	—	—	1	—	—	3	—	—	—	—	—	—	2	—	—	—	—	—
Lobianchia	—	—	—	—	—	1	—	—	—	2	3	4	—	—	—	—	—	—
Diaphus																		
theta	—	—	—	—	(5)	2	(4)	(7)	(8)	1	—	—	—	(9)	(3)	(6)	—	—
pacificus	—	—	—	—	—	2	(3)	(5)	—	1	(4)	—	—	—	(6)	—	—	—
Gymnoscopelus	—	—	—	—	—	2	4	—	—	1	—	—	—	—	3	—	—	—
Lampanyctodes	—	—	—	1	—	4	—	—	—	2	—	—	3	—	—	—	—	—
Scopelopsis	—	—	—	2	—	—	—	—	—	1	—	—	—	3	—	—	—	—
Lampichthys	—	—	—	2	—	4	—	—	—	1	—	—	3	—	—	—	—	—
Notoscopelus	—	—	—	2	—	—	—	—	—	1	—	—	3	—	—	—	—	—
Lampadena	—	—	—	3	—	3	—	—	—	2	—	—	1	—	—	—	—	—
Ceratoscopelus	—	—	—	1	—	—	—	—	—	3	—	—	2	—	—	—	—	—
Lepidophanes	—	—	—	1	—	—	—	—	—	1	—	—	1	—	—	—	—	—
Bolinichthys	—	—	—	(1)	—	—	—	—	—	(1)	—	—	(1)	—	—	—	—	—

ordinal relationships. One set is the size at various developmental milestones. Myctophid larvae hatch at about 2 mm length with a yolk-sac remnant. Notochord flexion occurs in a narrow size interval (0.5–2.0 mm) and the size at mid-flexion is typically about half the maximum larval size. Size at transformation also occurs within a short length interval, usually not exceeding 2 mm. Most myctophid species transform in the length range of 12–19 mm, although some (e.g., *Electrona rissoi, Notolychnus valdiviae*) are as small as 9–10 mm at transformation and some species of *Symbolophorus* reach about 23 mm before transformation. *Gymnoscopelus nicholsi* has the largest larvae recorded, up to 28 mm.

Head, body, and gut shape are distinctive for most species and within most genera there is a similarity of shape (Figs. 115–124). While most myctophid larvae are moderately slender, body shape can range from highly attenuate (e.g., *Hygophum reinhardti*) to markedly robust (e.g., some *Myctophum* and *Lampanyctus* species). Some are deep-bodied but laterally compressed (e.g., Gonichthyini). Robust larvae and deep-bodied, laterally compressed forms tend to have large heads and jaws, while attenuate forms have flat heads.

The eye is varied in size and shape and provides numerous characters. In the Myctophinae the eyes are elliptical in outline in contrast to most Lampanyctinae which have rounded eyes. Further specializations in Myctophinae are the presence of variously shaped choroid tissue on the ventral surface of the eye in most genera and eye stalks in several genera. Among lampanyctine genera eyes are sessile and only *Lobianchia dofleini* and species of *Triphoturus* have markedly narrowed eyes with choroid tissue.

The gut has distinctive transverse rugae and ranges from short, to elongate, to trailing free from the body. In most myctophids it extends to about the midpoint of the body and is slightly S-shaped. The curvature tends to be more pronounced in taxa with short guts. In two myctophine genera (*Metelectrona* and some *Hygophum* species) the anterior section of the gut is small in diameter and opens dorsally into the relatively larger posterior section.

In most myctophids, ray formation and ossification of fins proceeds in the following sequence: caudal, pectoral, anal, dorsal, and pelvic. However, in some *Symbolophorus* species the pelvic fin forms early and ossification of rays precedes that of the anal and dorsal fins. In most species the pectoral fin is relatively small, but deep-bodied and robust forms in both

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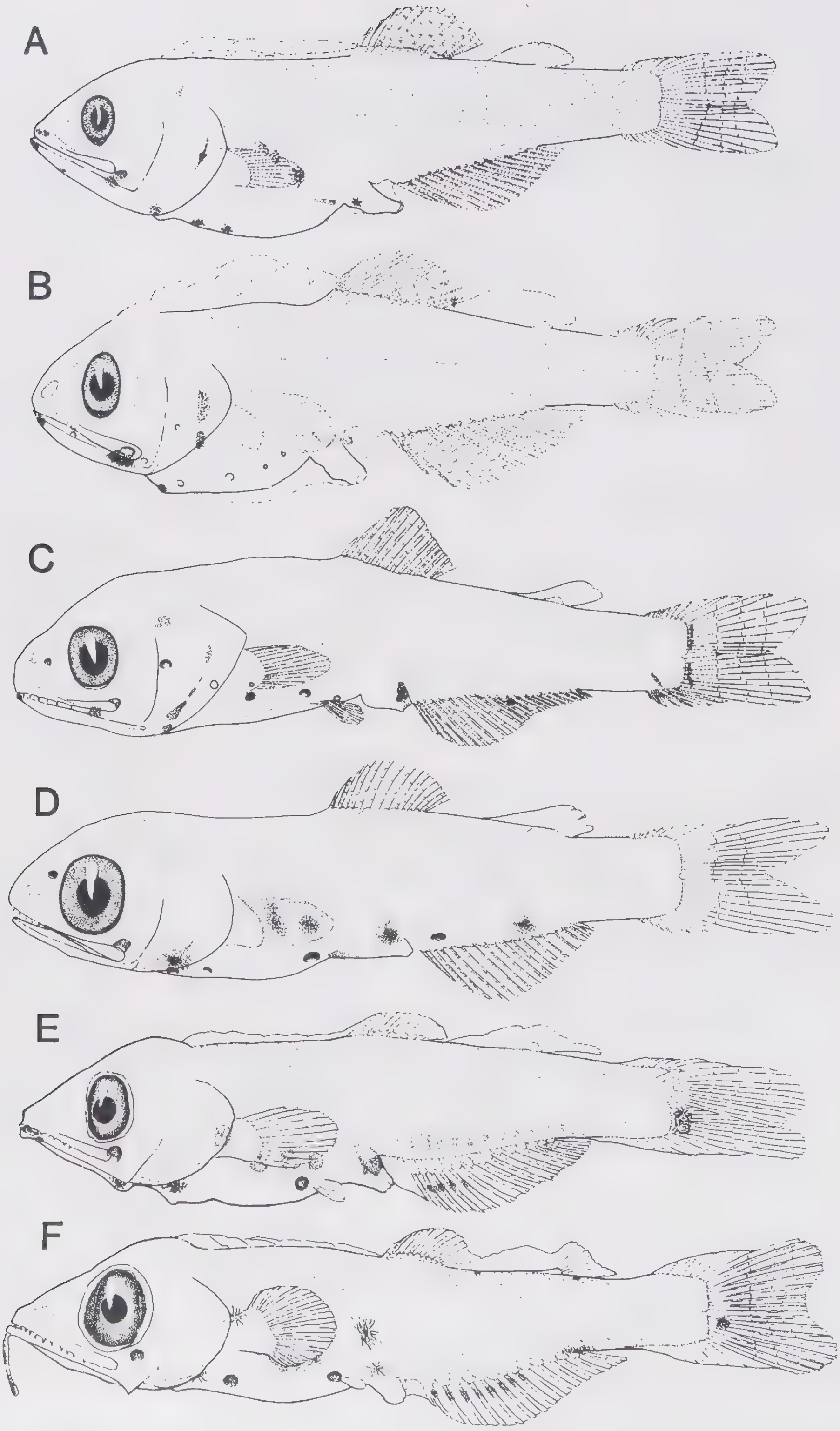
Fig. 116. Larvae of Myctophini. (A) *Benthosema glaciale*, 10.5 mm; (B) *B. suborbitale*, 9.2 mm; (C) *B. pterota*, 8.5 mm; (D) *B. fibulatum*, 8.7 mm; (E) *Diogenichthys laternatus*, 7.7 mm; (F) *D. atlanticus*, 8.8 mm. A–D from Moser and Ahlstrom (1974); E and F from Moser and Ahlstrom (1970).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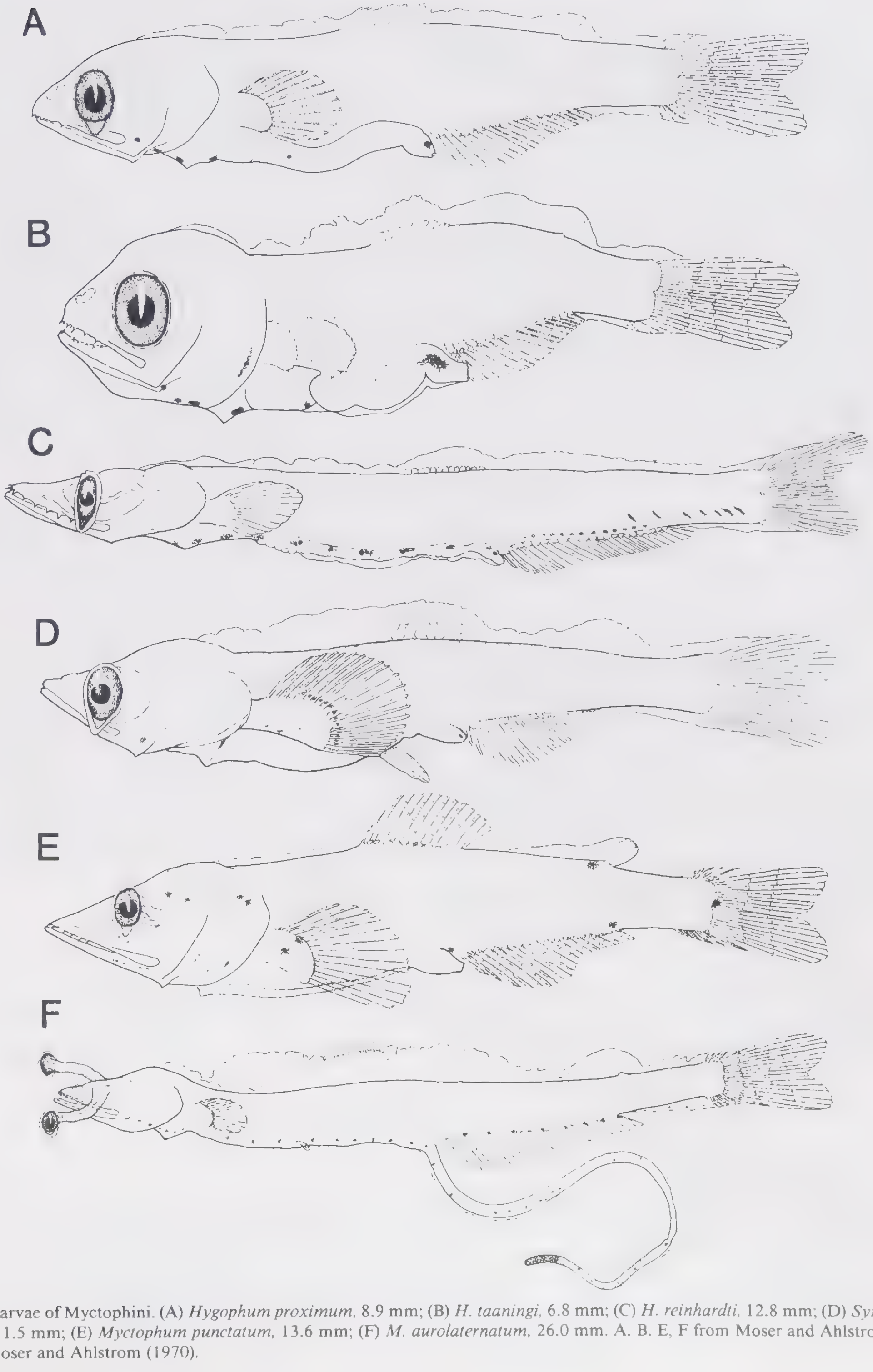

Fig. 117. Larvae of Myctophini. (A) *Hygophum proximum,* 8.9 mm; (B) *H. taaningi,* 6.8 mm; (C) *H. reinhardti,* 12.8 mm; (D) *Symbolophorus californiense,* 11.5 mm; (E) *Myctophum punctatum,* 13.6 mm; (F) *M. aurolaternatum,* 26.0 mm. A, B, E, F from Moser and Ahlstrom (1974); C and D from Moser and Ahlstrom (1970).

subfamilies have large fins and fin bases. In *Symbolophorus* the fin base is uniquely shaped and in *Lobianchia* the fin blade has a unique shape. In two genera (*Loweina, Tarletonbeania*) the lowermost pectoral ray is elongate and ornamented. The finfold is enlarged in many myctophine genera and greatly enlarged in one myctophine tribe, the Gonichthyini.

Myctophids, with the exception of *Notolychnus* and *Taaningichthys*, develop the middle branchiostegal photophore (Br_2) during the larval period. It is located posteroventral to the orbit but during transformation assumes a position beneath the orbit on the branchiostegal membrane. Three myctophine genera and 11 lampanyctine genera develop additional photophores during the larval period; however, the Br_2 is always the first to develop. The larval photophore complements and the sequence of appearance of constituent photophores are useful characters.

Myctophid species have distinct melanophore patterns, with the exception of the large genus *Diaphus*, for which only a few specific patterns have been identified. Most genera may be separated by overall similarity of pattern among their species and some have unique melanophore loci. There are no clear patterns for tribes or subfamilies although certain pigment loci are persistent in some tribes (e.g., caudal fin base spots in diaphines; dorsal midline series in gymnoscopelines).

In the following summary of key larval characters, the genera are listed for convenience as in Moser and Ahlstrom (1970, 1972, 1974) and the sequence does not necessarily imply relationship. Likewise, the species groups serve only to identify phenotypically similar larval types. Larvae of a majority of myctophid genera have a moderately slender body, a head of moderate size, with a slightly convex dorsal profile and a pointed snout of moderate length. Body and head shape are noted only when they depart from this morph. In Myctophinae eye shape is noted when it is markedly elliptical and size is noted only when larger or smaller than typical. In Lampanyctinae eye shape is noted only when it departs from the round condition and eye size only when larger or smaller than typical. Choroid tissue is described only when it is present. Gut length and shape are described only if there is a departure from the typical morph—a slightly S-shaped gut that extends to about midbody. The most persistent pigment locus in myctophid larvae is above or to the side of the free terminal section of the gut, thus only the lack of this pigment is noted. Larval photophores, in addition to the Br_2, and their sequence of appearance are shown in Table 62.

MYCTOPHINAE

Krefftichthys.—Fig. 115A; head small with short snout; conical choroid tissue; gut straight, extending beyond midbody; dorsal fin displaced posteriad; lateral gut and postanal median ventral melanophore series; large lateral hypural pigment patch.

Protomyctophum.—Fig. 115B, C; two subgenera; head small to moderate in size, gut short, wide space between anus and anal fin; head pigment lacking except in otic region of *P. Heirops chilensis*; some species may have melanophores on lateral gut, above gut on trunk, above gas bladder, in postanal ventral midline series, prominent pigment on lateral hypural region. *P. Heirops*: Fig. 115C; characters similar to *P. Protomyctophum* except eye narrower.

Electrona.—Fig. 115D, E; body moderately slender to moderatey deep; head moderately large; snout blunt or pointed; gut short, somewhat saccular, strongly S-shaped; space between anus and anal fin not as large as in *Protomyctophum*; three morphs. *E. subaspera-E. carlsbergi*: eye slightly elliptical, small lunate choroid mass in *E. carlsbergi*; pigment above gut; *E. subaspera* has pigment lateral to cleithrum. *E. rissoi*: Fig. 115D; head large, broad; eye very narrow; pigment at lower jaw symphysis, on pectoral fin blade. *E. antarctica*: Fig. 115E; body and head laterally compressed; gut mass protrudes ventrally from body profile; eye small, narrow, with bicolored elongate conical choroid mass; pigment on upper jaw, pectoral fin blade, lateral gut, lateral hypural region.

Metelectrona.—Fig. 115F; body and head laterally compressed; dorsal finfold enlarged with fin base initially separated from body; lunate choroid mass; anterior gut section with small diameter, opening dorsally into somewhat saccular posterior section; pigment below lower jaw and on isthmus.

Benthosema.—Fig. 116A–D; two morphs; photophores (Table 62). *B. glaciale-B. suborbitale*: Fig. 116A, B; eyes narrow, with small lunate choroid mass; gut moderately short in preflexion larvae with space between anus and anal fin; pigment on snout, lower jaw, hindbrain, lateral and ventral cleithral region; pigment above gut in *B. glaciale*. *B. pterota-B. fibulatum*: Fig. 116C, D; eyes less narrow than in above morph, with sliver of choroid tissue or none; gut extends to about midbody with no space between anus and anal fin; preflexion larvae with melanophore series on lateral gut and on postanal ventral midline, coalescing to a single melanophore; lateral cleithral pigment; lower jaw pigment in *B. pterota*.

Diogenichthys.—Fig. 116E, F; eyes very narrow in preflexion stage, less so in postflexion; photophores (Table 62); pigment series on lateral gut and on postanal ventral midline, increasing with development; spot at caudal fin base; pigment on tip of lower jaw in *D. laternatus*; *D. atlanticus* has spot on trunk above terminal gut flexure and pigment on symphyseal barbel.

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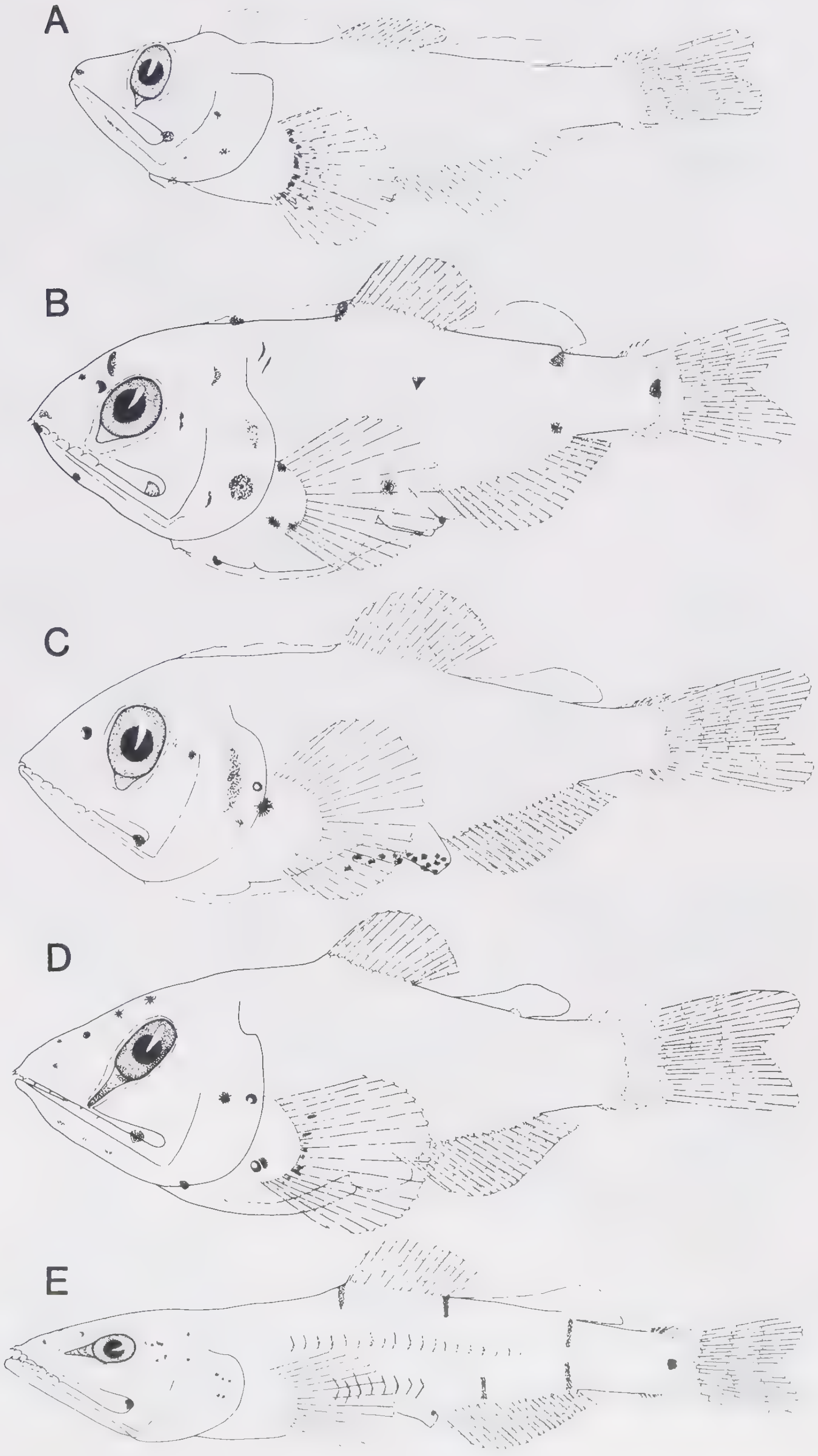
Fig. 118. Larvae of *Myctophum*. (A) *M. phengodes*, 9.8 mm; (B) *M. asperum*, 6.8 mm; (C) *M. brachygnathum*, 7.5 mm; (D) *M. selenops*, 7.8 mm; (E) *M. spinosum*, 9.0 mm. From Moser and Ahlstrom (1974).

Fig. 119. Larvae of Gonichthyini. (A) *Loweina rara*, 17.6 mm; (B) *Tarletonbeania crenularis*, 18.9 mm; (C) *Gonichthys tenuiculus*, 7.7 mm; (D) *Centrobranchus choerocephalus*, 7.3 mm. From Moser and Ahlstrom (1970).

Fig. 120. Larvae of Lampanyctinae. (A) *Notolychnus valdiviae*, 8.7 mm; (B) *Lobianchia dofleini*, 8.2 mm; (C) *L. gemellari*, 6.7 mm; (D) *Diaphus theta*, 6.9 mm; (E) *D. pacificus*, 5.2 mm; (F) *Gymnoscopelus nicholsi*, 23.5 mm. A–E from Moser and Ahlstrom (1974); F from Moser and Ahlstrom (1972).

Fig. 121. Larvae of Lampanyctinae. (A) *Lampanyctodes hectoris*, 13.0 mm; (B) *Scopelopsis multipunctatus*, 13.4 mm; (C) *Lampichthys procerus*, 14.5 mm; (D) *Notoscopelus resplendens*, 11.2 mm; (E) *Lampadena luminosa*, 12.8 mm; (F) *Taaningichthys minimus*, 14.4 mm. A from Ahlstrom et al. (1976); B, C, F from Moser and Ahlstrom (1972); D and E from Moser and Ahlstrom (1974).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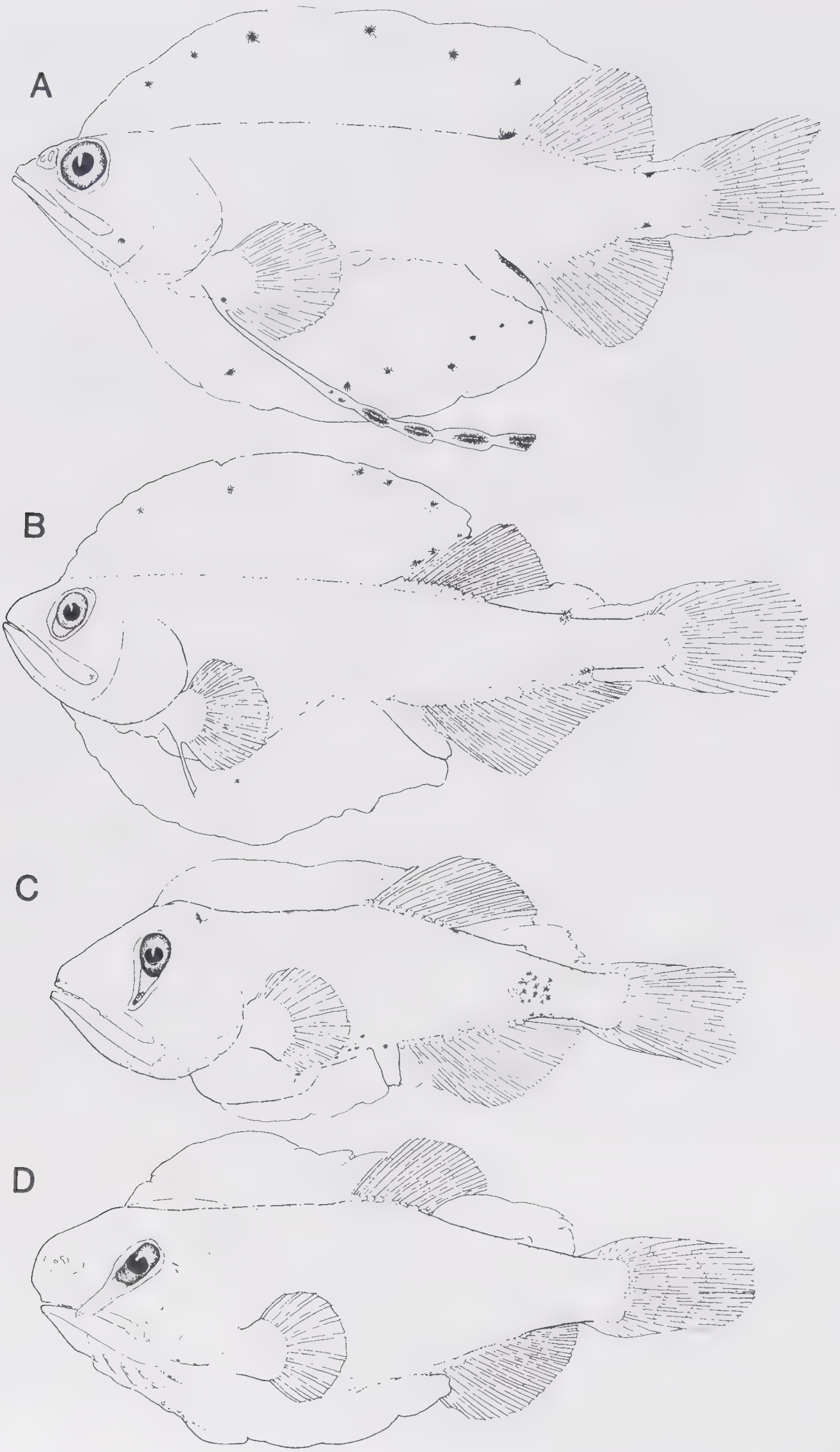
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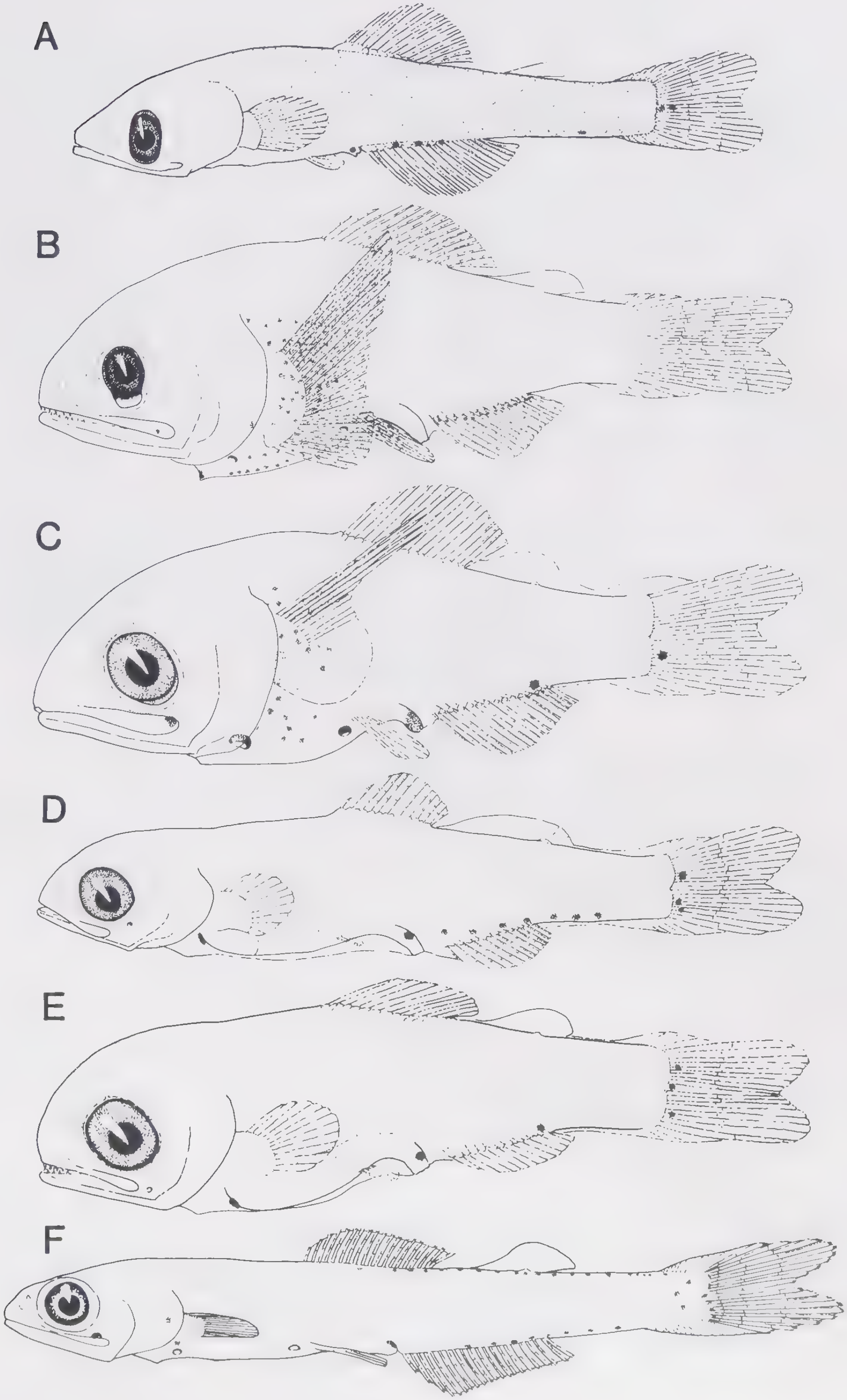
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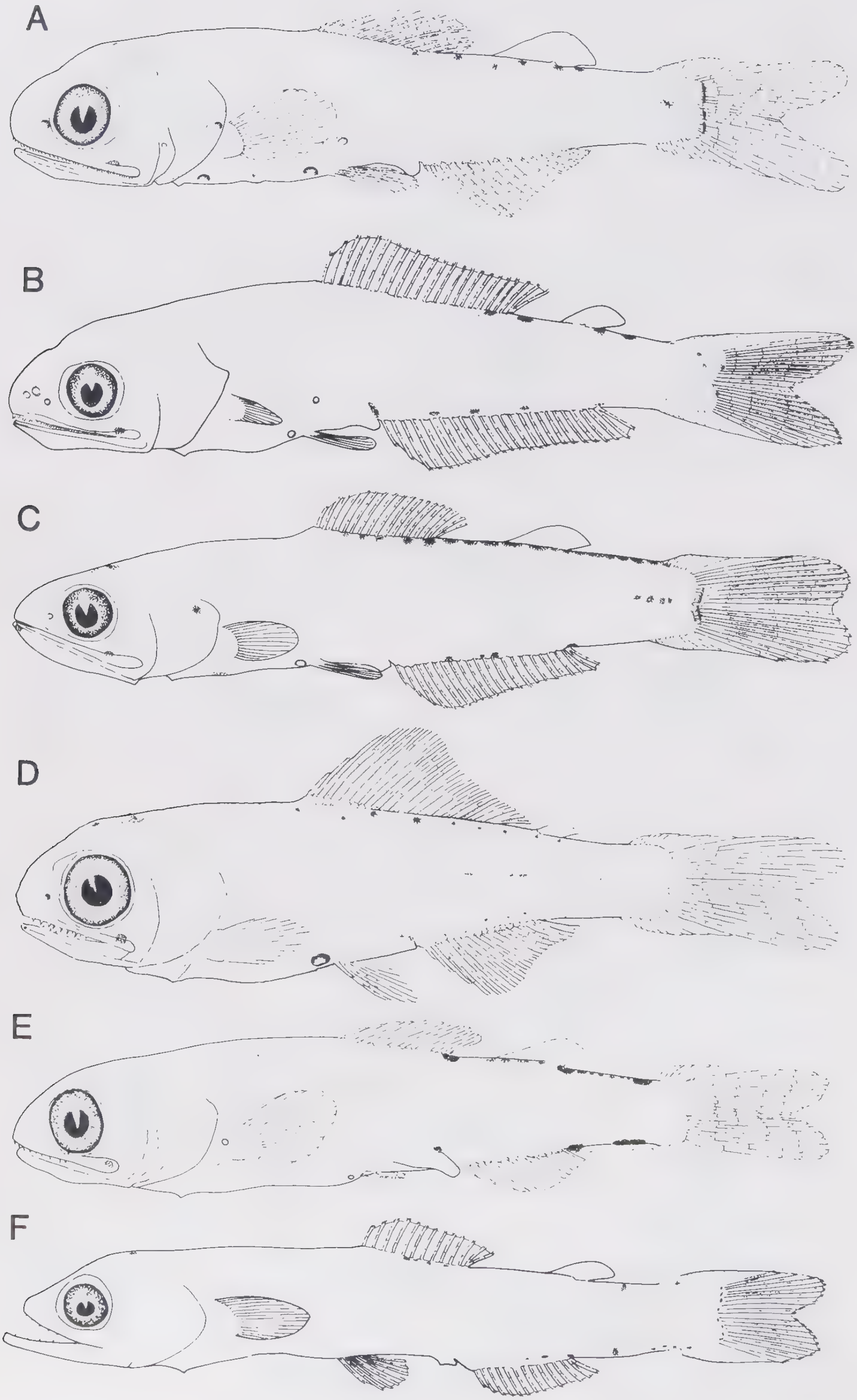
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Hygophum.—Fig. 117A–C; diagnostic pattern of melanophores at the cleithral symphysis and isthmus region consisting of paired pigment dashes that form a median line as the series extends forward on the isthmus; Br_2 photophore forms late in larval period; three morphs. *H. proximum-H. hygomi-H. benoiti-H. hanseni-H. brunni*: Fig. 117A; eye moderately narrow with conical choroid tissue; pigment sparse in most species with some lateral gut spots in all species; some species may have pigment on hypaxial myosepta, jaws, lateral cleithral region, base of caudal rays. *H. atratum-H. reinhardti*: Fig. 117C; body very slender; head flat; eyes very narrow, on short stalks; elongate conical choroid mass; gut almost straight, small diameter; pigment series along lateral gut and hypaxial myosepta; pigment at caudal fin base; pigment on lower jaw symphysis in *H. atratum*. *H. macrochir-H. taaningi*: Fig. 117B; body and head deep and laterally compressed; eyes large, relatively wide; no choroid tissue; anterior gut section narrow in diameter, opening dorsally into somewhat saccular posterior section; *H. macrochir* has pigment on upper and lower jaw and a patch of melanophores on posterior gut section; *H. taaningi* has pigment on gular region and lateral surface of cleithrum.

Symbolophorus.—Fig. 117D; head broad, somewhat flat; eyes slightly stalked, conical choroid mass; pectoral fin large with supernumerary rays, base wing-shaped, rays ossify early; pelvic fin large, early-forming in some species; dorsal finfold well developed with fin base forming in it; pigment series on lateral gut and postanal ventral midline in preflexion larvae; pigment on snout, hindbrain, lateral cleithral region, isthmus, paired fins.

Myctophum.—Figs. 117E, F and 118A–E; at least five distinct morphs, all but *M. aurolaternatum* with enlarged fan-shaped pectoral fins, some with supernumerary rays and early ossification; conical choroid mass. *M. aurolaternatum*: Fig. 117F; body very slender; head somewhat flat; eyes small, on elongate stalks; gut straight, at midbody becomes trailing, extending to well beyond caudal fin; dorsal finfold well developed, fin base forms at its margin; pigment series on lateral gut, evenly distributed on trailing section, except heavier near terminus; pigment on jaws, isthmus, opercle, branchiostegal membrane, pectoral fin, anal fin base, caudal fin. *M. nitidulum-M. punctatum*: Fig. 117E; body moderately slender to slightly deep; head broad, somewhat flat in preflexion stage; eyes on short stalks; numerous small melanophores on snout, jaws, brain, isthmus, branchiostegal membrane; two rows of melanophores on ventral surface of gut; opposing melanophores on postanal dorsal and ventral midline; pigment on pectoral fin base and blade and at base of caudal rays. *M. phengodes*: Fig. 118A; body and head moderately deep; similar to *M. nitidulum,* except pigment sparse and eyes not stalked; pigment at base of pectoral fin rays. *M. spinosum-M. lychnobium*: Fig. 118E; head with convex dorsal profile and long snout giving the larva a fusiform appearance; long axis of eye rotated towards horizontal; photophores (Table 62); head heavily pigmented on jaws, brain, postorbital and opercular regions; pigment above gut on trunk, embedded in myosepta in *M. spinosum*; opposing dorsal and ventral midline blotches, larger and more deeply embedded in *M. spinosum* with embedded myoseptal pigment along horizontal septum; blotch at base of caudal rays. *M. asperum-M. brachygnathum-M. obtusirostre-M. selenops*: Fig. 118B–D; body deep, robust; head broad, deep with convex dorsal profile and large snout; eye relatively larger than in other morphs; choroid tissue broadly conical, except in *M. selenops* where it is elongate and pigmented at tip; photophores (Table 62); head pigment similar to *M. spinosum*; most species have heavy pigment lateral to cleithra and on pectoral fin bases; all species lack trunk and tail pigment, except *M. asperum* which has extensive embedded myoseptal and dorsal/ventral midline blotches.

Loweina.—Fig. 119A; body and head moderately deep, laterally compressed; dorsal and anal fins displaced far posteriad; dorsal and ventral finfolds greatly enlarged and conspicuously pigmented to produce a disc-shaped profile; eyes large; gut with expanded anterior section and enlarged terminal section; pectoral fin large with lower-most ray elongate, ornamented with pigmented spatulations; interorbital pigment band; pigment at lateral cleithral surface, dorsal fin origin, and opposing midline blotches at caudal peduncle region.

Tarletonbeania.—Fig. 119B; similar to *Loweina,* except median fins displaced less posteriad; eye narrower and with lunate choroid mass; four melanophores on periphery of brain, two melanophore series on ventrum of gut.

Gonichthys.—Fig. 119C; body and head deep and laterally compressed, leaf-like; snout large, angulate in profile; eye small with elongate conical choroid mass, pigmented at tip; enlarged dorsal and ventral finfolds; pectoral fins moderately large; pigment on snout, jaws, midline of brain, postorbital and opercular regions; pigment on lateral hindgut and on trunk above gut; series of embedded blotches on dorsal midline of body, opposing blotches on postanal ventral midline; large pigment patch on lateral caudal peduncle region in *G. tenuiculus*; heavy embedded pigment streak along horizontal septum in *G. coccoi.*

Centrobranchus.—Fig. 119D; morphology similar to *Gonichthys* except snout markedly blunt and rounded and terminal gut flexure less acute; two morphs. *C. choerocephalus-C. brevirostris-C. nigroocellatus*: Fig. 119D; eye very narrow with unpigmented choroid mass that exceeds it in length; pigment sparse; some at postorbital-opercular region, branchiostegal membrane, ventral surface of liver. *C. andrae*: eye wider than in above morph and with short conical choroid mass; pigment extensive, on snout, upper jaw, dorsal brain, opercle, branchiostegal membrane, lateral hindgut, ventral surface of liver, pectoral fin base; embedded spots along dorsal midline with opposing spots along postanal ventral midline; embedded spots along horizontal septum in caudal peduncle region.

Lampanyctinae

Notolychnus.—Fig. 120A; head relatively large with moderately elongate snout; eyes usually narrow, often irregular in shape; gut short, more so in preflexion stage; no photophores, even Br_2 lacking; pigment on lateral hindgut, gas bladder, base of caudal rays; a persistent but sparse postanal ventral midline series.

Lobianchia.—Fig. 120B, C; body deep, robust; head broad with large snout; pectoral fins large; blade wing-shaped with upper rays longer than others; photophores (Table 62); head unpigmented; pigment on trunk, on gut below pectoral fin base, on pectoral fin base and blade, embedded in gut region anterior to pectoral fin base, along anal fin base, and at base of caudal rays; embedded melanophores in myosepta above pectoral fin becoming extensive in postflexion stage; two morphs. *L. dofleini*: Fig. 120B; eye small, narrow, with lunate to squarish choroid

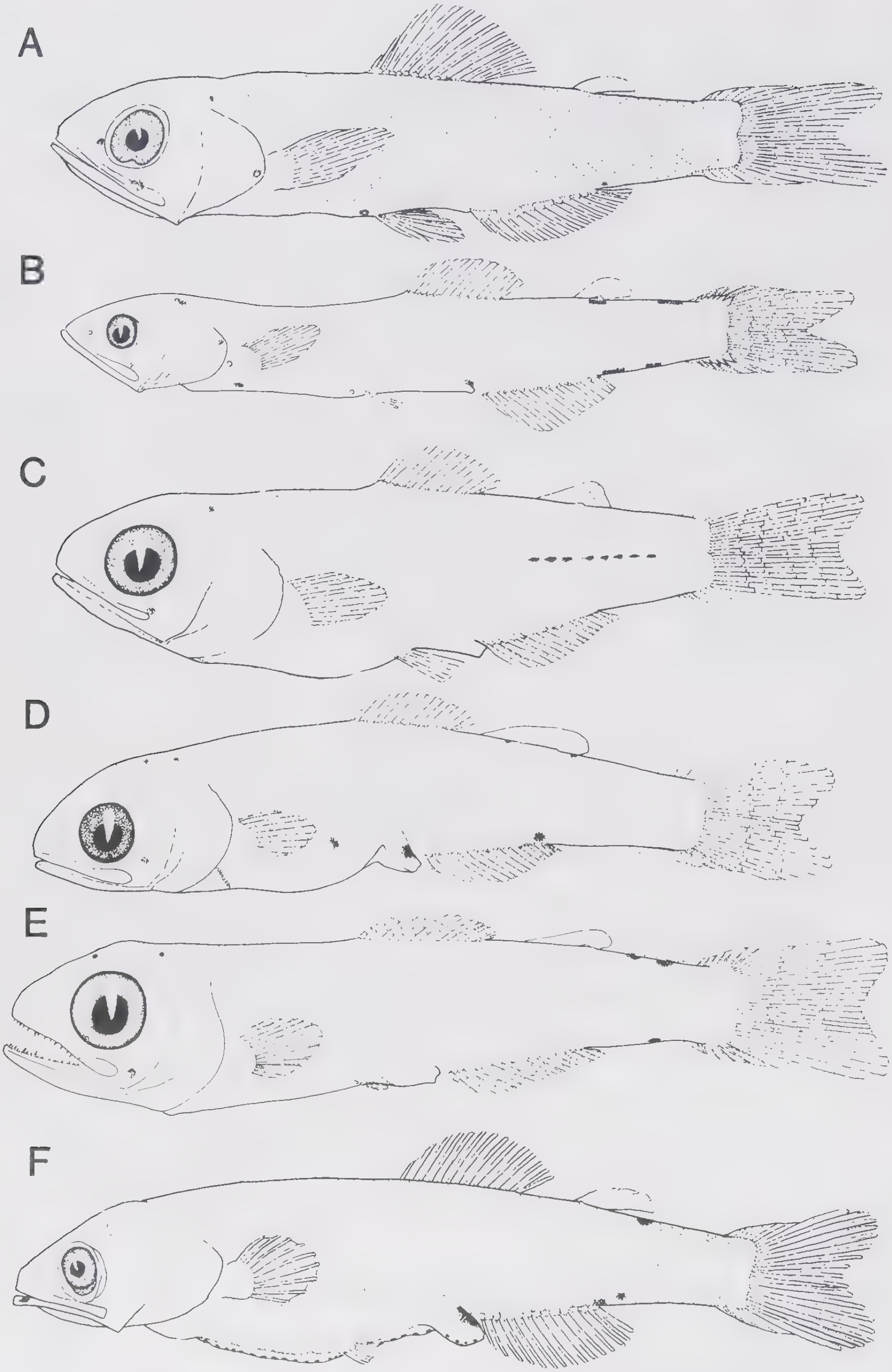


Fig. 122. Larvae of *Lampanyctinae.* (A) *Ceratoscopelus townsendi,* 16.6 mm; (B) *Lepidophanes gaussi,* 13.5 mm; (C) *Bolinichthys distofax,* 9.4 mm; (D) *Stenobrachius leucopsarus,* 10.4 mm; (E) *Parvilux ingens,* 14.4 mm; (F) *Triphoturus mexicanus,* 10.5 mm. A–E from Moser and Ahlstrom (1974); F from Ahlstrom (1972b).

mass; gradual transition from lower pectoral rays to longer upper rays. *L. gemellari*: Fig. 120C; eye large, almost round, choroid mass a lunate sliver; abrupt transition between lower pectoral rays and long upper rays.

Diaphus.—Fig. 120D, E; pigment lacking on head; melanophore at anteroventral surface of liver, one or more at midgut region, one or more at base of caudal rays; gas bladder pigmented; two morphs. *D. theta*: Fig. 120D; body moderately slender; head moderate in size; photophores (Table 62); numerous melanophores in postanal ventral midline series, persisting into postflexion stage. *D. pacificus*: Fig. 120E; body moderately deep, somewhat robust; head moderately large; photophores (Table 62); a few melanophores in postanal ventral midline series, usually coalescing to one before flexion stage.

Gymnoscopelus.—Fig. 120F; photophores (Table 62); pigment above brain, at lateral cleithral region, above midgut, above gas bladder; postanal ventral midline series present but, in some species, restricted to caudal peduncle region; melanophore series on each side of dorsal midline, in most species extending between caudal and dorsal fins, in others extending forward to dorsal fin origin, and in others restricted to caudal penduncle region; pigment at base of caudal rays; some species have pigment on lateral hypural region; lateral pigment patch at caudal peduncle in *G. opisthopterus,* which also has embedded melanophores above vertebral column.

Lampanyctodes.—Fig. 121A; photophores (Table 62); pigment above brain, at anteroventral surface of liver, above gas bladder; a postanal ventral midline series and a series on each side of dorsal midline between dorsal and caudal fins; pigment at base of caudal rays and at lateral hypural region.

Scopelopsis.—Fig. 121B; photophores (Table 62); pigment similar to *Lampanyctodes* except additional melanophores on hindbrain, nape, lateral cleithral region; pigment rows along dorsum irregular.

Lampichthys.—Fig. 121C; photophores (Table 62); pigment similar to *Scopelopsis* except dorsal rows consist of large closely-spaced melanophores which at maximal development extend from caudal fin to dorsal fin origin; a short melanophore series along horizontal septum on caudal peduncle in late postflexion stage.

Notoscopelus.—Fig. 121D; photophores (Table 62); body moderately deep; head moderately large; eye large; snout becomes somewhat bulbous at flexion stage; gut short in early preflexion stage, elongates to about midbody by late preflexion; pigment at tips of jaws, above brain, above gas bladder and at lateral cleithral region in early postflexion larvae; additional pigment develops below lower jaw, on hindbrain and nape; series of melanophores on each side of dorsal midline, beginning at midbody and gradually developing along entire dorsum; series along horizontal septum and along anal fin base; pigment on base of caudal rays and on pelvic and anal rays in some species at late postflexion stage; extensive embedded myoseptal pigment on trunk or tail in postflexion stages of some species.

Lampadena.—Fig. 121E; photophores (Table 62); pigment above brain, nape, gut, gas bladder; most species have large melanophores along dorsal midline, with opposing postanal ventral midline melanophores; some species with smaller, more numerous melanophores in dorsal and ventral series; embedded pigment above spinal column in some species.

Taaningichthys.—Fig. 121F; body slender; lower jaw projects beyond upper; no photophores, even Br_2 lacking; pigment above brain, in otic region, one to several opposing melanophores at postanal dorsal and ventral midline; late postflexion larvae may develop minute melanophores along each side of dorsal midline; pigment at base of caudal rays; series of embedded melanophores above spinal column.

Ceratoscopelus.—Fig. 122A; eye elliptical in early larvae; photophores (Table 62); pigment above gut; postanal ventral midline series in early larvae, coalesces to a single spot in postflexion larvae; *C. maderensis* has short series at dorsal and ventral midline in caudal peduncle region; embedded pigment above posterior region of spinal column in some species.

Lepidophanes.—Fig. 122B; eye small; photophores (Table 62); usually two melanophore pairs at dorsal midline in caudal peduncle region and one or two ventral midline melanophores; *L. gaussi* has median melanophore above hindbrain and median ventral melanophore below pectoral fin base.

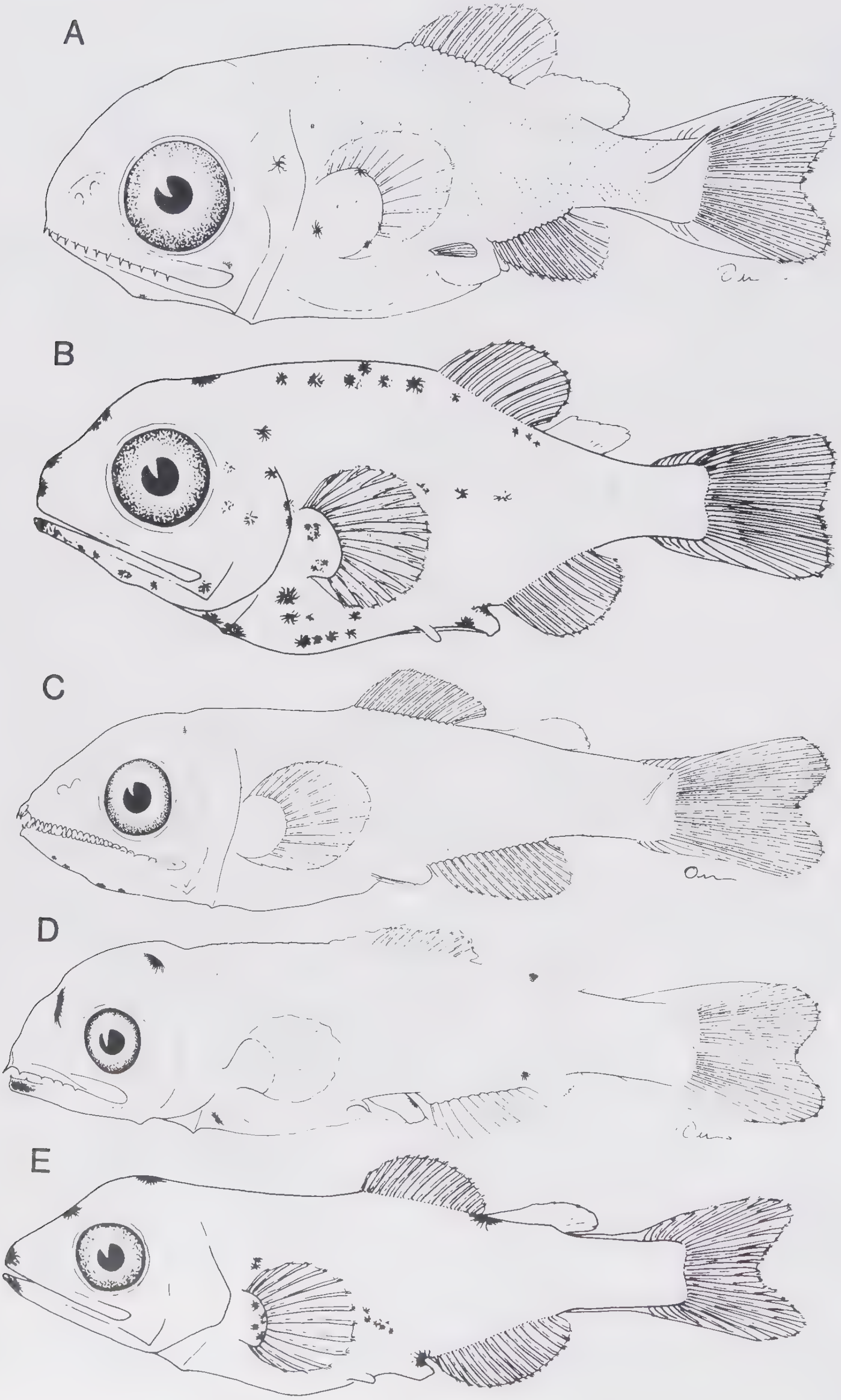
Bolinichthys.—Fig. 122C; moderately deep-bodied; snout blunt; eye large; photophores (Table 62); sparse pigment; midline spot above brain, embedded otic spot, embedded pigment above gut; some species with a sparse postanal median ventral series that coalesces to a single melanophore; *B. distofax* has a short series on horizontal septum; embedded pigment above posterior region of spinal column in some species.

Triphoturus.—Fig. 122F; eye elliptical with choroid mass; pigment at tip of lower jaw, at angular region of jaw, at lateral cleithral region; early preflexion larvae have paired lateral gut spots near pectoral fin base and at midgut; anterior pair coalesces to a median position anteroventral to liver, the posterior pair becomes dorsal to gut; pigment above gas bladder; early preflexion larvae have postanal median ventral series that coalesces to one or two spots; pigment along margin of preanal finfolds; a single dorsal spot at adipose fin in *T. mexicanus*; a series of pigment dashes on horizontal septum in *T. nigrescens.*

Stenobrachius.—Fig. 122D; gut melanophores and postanal median ventral series similar to *Triphoturus*; pigment above brain and nape in postflexion stage; late postflexion larvae have embedded melanophores in trunk myosepta and melanophore series on each side of dorsal midline.

Parvilux.—Fig. 122E; head, eyes large; tapered body; gut short

Fig. 123. Larvae of *Lampanyctus.* (A) *L. steinbecki,* 6.6 mm; CalCOFI Sta. 70.200; (B) *L. pusillus,* 7.7 mm; redrawn from Taaning (1918); (C) *L. nobilis,* 9.6 mm; SEFC, OR II 7343 Sta. 98; (D) *L. parvicauda,* 7.5 mm, SWFC, Eastropac Op Sta. 023; (E) *L. crocodilus,* 11.5 mm, redrawn from Tåning (1918).


A
B
C
D
E

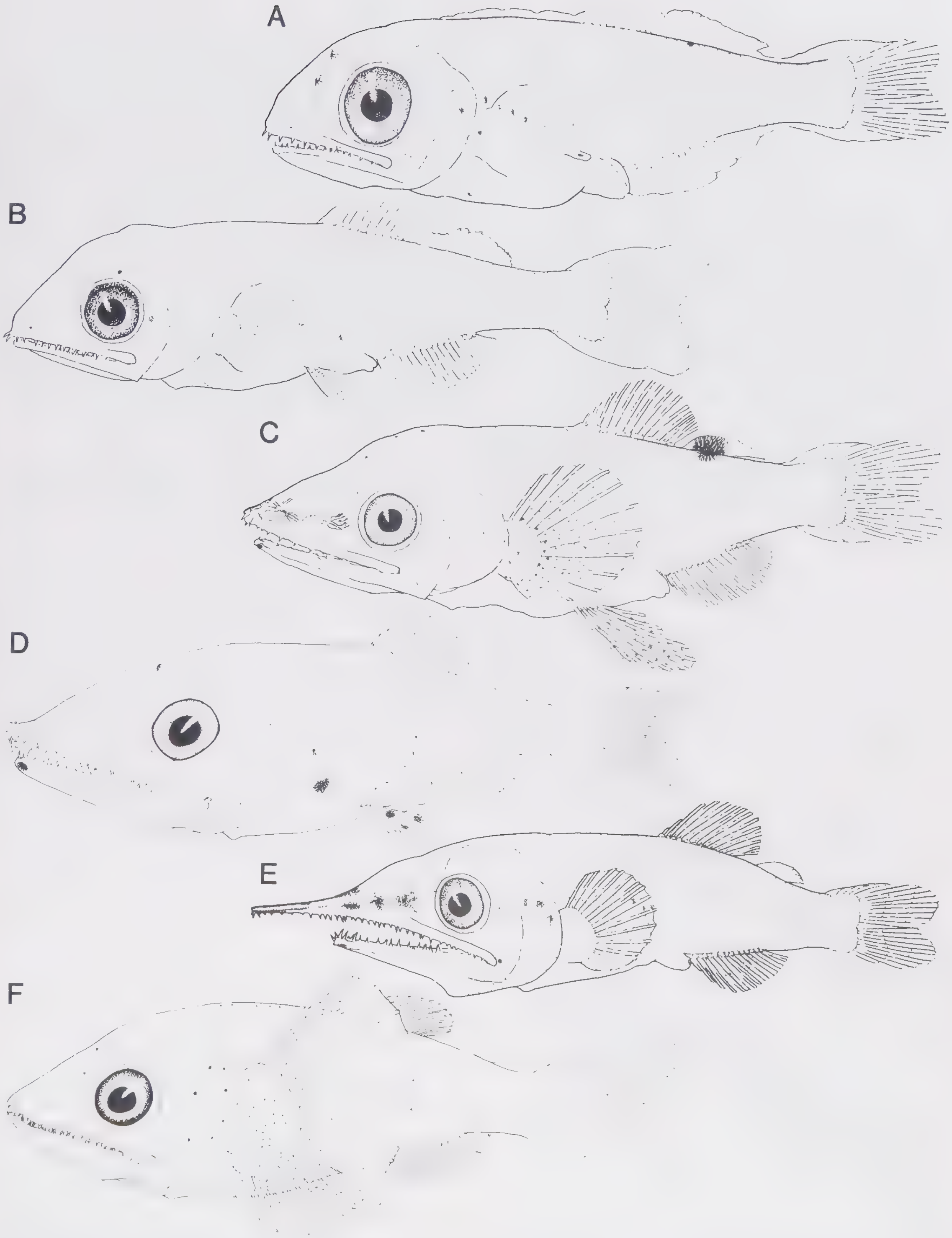


Fig. 124. Larvae of *Lampanyctus*. (A) *L. ritteri*, 10.1 mm; (B) *L. idostigma*, 7.2 mm, CalCOFI 6002 Sta. 133.45; (C) *L. regalis*, 13.0 mm; (D) *Lampanyctus* sp., 8.7 mm; (E) *L. achirus*, 13.4 mm; (F) *Lampanyctus* sp., 9.4 mm. A, C, D, E from Moser and Ahlstrom (1974); F from Moser (1981).

in early preflexion stage, elongates to midbody by flexion stage; in postflexion stage pigment above brain, embedded in otic region, lateral to cleithrum, at anteroventral region of liver; one to several dorsal median melanophores and one ventral median melanophore at caudal peduncle.

Lampanyctus.—Figs. 123, 124; body slender; head deep; gut short in early preflexion stage; during preflexion stage gut lengthens to midbody, body deepens and becomes somewhat robust in most species; pigment above brain in most species; postflexion larvae develop trunk myoseptal pigment that increases to cover most of the anterior trunk at transformation; at least 6 morphs. *L. nobilis-L. parvicauda-L. omostigma-L. crocodilus-L. ritteri-L. idostigma*: Figs. 123C–E, 124A, B; body and head moderately deep; eyes, jaws, pectoral fins moderate in size; pigment may be present at snout, lower jaw, opercle, above gut, anteroventral surface of liver, at dorsal or ventral midline on tail. *L. pusillus-L. steinbecki*: Fig. 123A, B; deep, broad body and head, very robust; snout blunt; eyes large; dorsal and anal fins displaced posteriad; pectoral fins moderately large; *L. pusillus* heavily pigmented on head, body, pectoral fin base; series along horizontal septum; *L. steinbecki* with pigment below lower jaw, on opercle, pectoral fin base; series along horizontal septum and embedded pigment on tail in postflexion larvae. *L. regalis-L. ater*: Fig. 124C; deep, large head and body; snout elongate, jaws large, teeth well developed, especially at tip of upper jaw; preopercular spines in some species; dorsal and anal fins displaced posteriad; pectoral fins moderate to large; pigment may be present at tips of jaws, embedded in snout, at postorbital and opercular regions, pectoral and pelvic fins; spot at adipose fin in *L. regalis*; one or two dorsal spots in *L. ater*. Information on *L. ater* from H. Zadoretsky (Dept. Zoology, Univ. of Rhode Island, pers. comm.). *L. achirus*: Fig. 124E; body moderately deep; head and jaws large with snout produced into toothy rostrum; dorsal and anal fins displaced posteriad; pectoral fins moderately large; pigment on tips of jaws, embedded in snout, and present at postorbital and opercular regions. *L. lineatus-L. cuprarius*: body moderately elongate; snout elongate, jaws large; head pigment as in *L. achirus*; *L. lineatus* pigment consists of numerous melanophores along dorsum and ventrum and at base of caudal rays; *L. cuprarius* has pigment above gut and an irregular bar below dorsal fin. Information from H. Zadoretsky (pers. comm.).

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CALIBRATION OF DENTAL LAYERS IN SEVEN CAPTIVE HAWAIIAN SPINNER DOLPHINS, *STENELLA LONGIROSTRIS*, BASED ON TETRACYCLINE LABELING

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ABSTRACT

To calibrate dentinal and cemental growth layer groups (GLGs) with real time, a study was conducted on the teeth from seven captive Hawaiian spinner dolphins that had been treated clinically with tetracycline (TCL) at numerous times over multiple years at Sea Life Park, Hawaii. To monitor layer accumulation as it occurred for 1 year, we gave single injections to three animals every 3 months and pulled a tooth from each every 6 months. By comparing dental-layer patterns between TCL labels that had been introduced at 6-month and 1-year intervals, annual patterns were distinguished. In the dentine, a thin, light layer (the first being the neonatal line) was formed about every 6 months. Each annual GLG contained 13 lunar monthly layers (LMLs). Using LML or light-layer counts, age, month, and year of birth were estimated for each of the seven specimens. All seven deposited nearly the same dentinal GLG thickness in the same year of life. Estimates of birth months indicated that five of the animals were born in late summer or early autumn and two were born in spring. Comparisons of dentinal labels with clinical records for a captive-born animal showed that TCL given to its mother was imparted via milk to the nursing calf. Time calibration of cemental GLGs showed that usually one cemental GLG was deposited annually, but in some cases a GLG was formed every second year or twice a year.

The technique of "reading" layers or growth layer groups (GLGs, terminology of Perrin and Myrick 1980) in teeth, developed to determine ages for pinnipeds in the early 1950's by Scheffer (1950) and Laws (1952), is now used routinely in dolphin studies (see reviews by Klevezal' and Kleinenberg 1967; Jonsgård 1969; Scheffer and Myrick 1980). Early work on dolphins (e.g., Nishiwaki and Yagi 1953; Sergeant 1959), showing a correlation between apparent age and number of GLGs led to the working assumption that GLG-deposition cycles are constant, each GLG usually, but not always, interpreted as representing 1 yr. Critical analysis of this assumption has been impaired by a lack of suitable material.

Three approaches have been used in efforts to calibrate dental GLGs with time and to determine their deposition rate: 1) In vivo labeling of tooth layers, 2) multiple extractions of teeth over time, and 3) examination of teeth from animals of known age. Nishiwaki and Yagi (1953) labeled the layered dentine in four wild-caught striped dolphins, *Stenella coeruleoalba*, by intramuscular injection of lead acetate paste. None of the four survived long enough for the labels to provide useful data.

Nielsen (1972) treated a young wild-caught harbor porpoise, *Phocoena phocoena*, with tetracycline (TCL) three times over a 370-d period. Three fluorescent labels were found in thin sections of its teeth examined in ultraviolet (UV) light "... but the uniform [unlayered] dentine made it impossible to determine the number of growth-layers formed per year" (Nielsen 1972:72).

Best (1976) administered oral doses of TCL hydrochloride, "Mysteclin-V", on each day over an 8-d period to each of three wild-caught dusky dolphins, *Lagenorhynchus obscurus*. Labels were detected in teeth of two of the three specimens after their deaths. In one specimen, dentine accumulated for 703 d between treatment and death averaged 200 μm/yr and 0.56 μm/d. In the other (older) specimen, the average deposition rate in dentine between the treatment label and the pulp-cavity wall was 77 μm/yr and 0.21 μm/d. Best concluded that the thickness of GLGs decreases significantly with age in dusky dolphins.

Gurevich et al. (1980) successfully introduced a single TCL label into the teeth of three of four wild-caught adult common dolphins, *Delphinus delphis*. The three labeled animals died 328, 354, and 441 d, respectively, after the date of treatment. By estimating the dentinal pattern laid down in about 1 yr, the investigators characterized an annual GLG. They estimated the ages of the animals by assuming that the GLGs in the unlabeled regions of the teeth rep-

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resented the same amount of time as the single GLG interpreted from the labeled region of each tooth.

A study by Hui (1978) included two tooth extractions made 2.5 yr apart from a captive male bottlenose dolphin, *Tursiops truncatus* (No. 10, "Kona"). Comparisons of longitudinal thin sections of the two teeth led Hui to conclude that " . . . almost three dentin layers [GLGs] had been deposited during the intervening period. . . " (p. 11). Other than indicating GLG boundaries in figures of the two thin sections (his fig. 3), Hui did not describe the GLGs or their components.

Three published studies (Sergeant 1959; Sergeant et al. 1973; Hui 1978) have attempted to demonstrate time content in GLGs using teeth of known-age, i.e., captive-born dolphins. All three had access to only a small number of specimens, all of *Tursiops truncatus*. Apparently, the investigators knew the ages of the specimens before defining and counting dentinal GLGs in the teeth, and no assurance was provided that the GLGs counted corresponded to annual periods between birth and death. Hui's study demonstrated that GLGs may be defined in such a manner as to verify the age that is already known for a specimen (Myrick 1980a). The incorrect age data (3.3 yr) provided to Hui for one of two "known-age" specimens studied by him (Hui 1978) led to his subsequent division of its dentinal layering pattern into three GLGs and a small fraction (Hui[4]). The original clinical records for the specimen (Hui's No. 29, LACM 54698) show, however, that the dolphin was born on 28 August 1965 and died on 8 August 1969, at nearly 4 yr of age.

Used independently, teeth of known-age animals, single-labeled teeth, or teeth extracted on two dates do not provide reliable means by which to determine tissue accumulation rates fully or to define GLGs with precision. Each method yields only two dates bracketing a segment of layered tissue into which the known elapsed time is divided. Myrick (1980b) described approaches that combine the use of two or more labels and two or more tooth extractions over an extended period to monitor rates and calibrate GLGs. The present paper is an account of such a study which used TCL-labeled teeth from seven captive Hawaiian spinner dolphins, *Stenella longirostris*.

MATERIALS AND METHODS

The study consisted of two phases. The first was a retrospective examination of TCL labels in the dolphins' dental tissues produced incidentally by clinical treatments administered during their captivity at Sea Life Park, Hawaii. Teeth were used from four frozen carcasses (Nos. WFP 606, 669, 670, and 671[5]), including one specimen of known age, and three live animals (Nos. ACM 103, 104, and 106) from which teeth were extracted in early 1980.

The second phase was a 1-yr monitoring of tissue-accumulation rates in teeth of three live animals. Each animal was given intramuscular injections of TCL at about 3-mo intervals and underwent three tooth extractions during the monitored period.

To restrain the dolphins during injections and extractions, an elevated rigid litter was placed near the edge of the dolphin holding tank in which the water level had been lowered to a depth of 0.5 m. The sloped tank bottom inclined the litter at an angle of 20° relative to the water surface. Each dolphin in turn was guided on its belly onto the litter until the front half of its body was above the water surface. In this position the dolphin could be held firmly with little apparent discomfort to the animal.

The procedure used to extract teeth was adapted for the spinners from the method described by Ridgway et al. (1975) for bottlenose dolphins. The dolphin's mouth was held open by moistened rolled toweling placed around the upper and lower jaws. Carbocaine[6] (5-10 cc) was injected into the right or left interalveolar nerve immediately behind the anterior border of the mandibular foramen. After allowing about 10 min for the anesthetic to take effect, a tooth was removed from the middle of the corresponding mandibular tooth row using an elevator and an extractor. The vacated alveolus was packed with cotton soaked with a ferric solution to control bleeding and promote healing.

Liquamycin 100, a form of TCL, was injected into the dorsal musculature between the dorsal fin and the blow hole. To reduce the possibility of local inflammation of the tissue—a problem known to result from concentrations of TCL—each dose (25 mg/kg body weight) was distributed along the dorsum at three separate sites.

Untreated (cut or ground) thin sections and decalcified and haematoxylin-stained (D/S) thin sections are the two most widely used preparations for dolphin teeth in age determination studies (see Perrin and Myrick 1980: 21 ff.). D/S sections produce simpler, more uniform GLG patterns, but de-calcification removes TCL labels (Nielsen 1972). We prepared the spinner teeth using both methods.

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[4] Clifford Hui, Naval Ocean Systems Center, San Diego, Calif., pers. commun. 1981.

[5] Skeletons are in the synoptic collection at Southwest Fisheries Center, NMFS, La Jolla, Calif.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Untreated, mid-longitudinal thin sections, 100 μm thick, were prepared by hand grinding and polishing teeth using 240 and 600 grit Al_2O_3 on a glass plate. Other teeth were decalcified in RDO[7] for 6-8 h, rinsed, and cut with a microtome in longitudinal plane to produce 30 μm thick sections that were stained in Mayer's haematoxylin for 15-30 min. Untreated and D/S preparations were mounted on slides in Permount or glycerin gel and covered with coverslips.

To determine the pattern components of GLGs, the D/S and untreated thin sections were examined in plain transmitted light 39× and 150× with a Zeiss photomicroscope. TCL labels were viewed at the same magnifications with UV reflected light using a Zeiss fluorescent vertical illuminator with a filter-reflector No. 44-75-05 combination attached to the same instrument.

Retrospective Calibration of Dentinal GLGs

Dates and durations of treatment, date of birth (for one specimen) or capture, and dates of death (for four carcasses) were taken from clinical records maintained for each dolphin during its captive life at Sea Life Park (for summaries see Myrick et al. in press). Data for each specimen were transcribed onto a calibration chart as the chronological series of event blocks, the relative width of a given block corresponding to the length of a given period of treatment.

In each thin section showing distinct fluorescent labels under UV light, label thicknesses and interlabel distances were measured. Label-measurement data for each dolphin were entered on its chart as a series of blocks below the event blocks, with spacing and thickness scaled to the corresponding measurements. The treatment and label blocks were compared for spacing and thickness to identify the date each label was introduced. Connecting lines were drawn from the beginning and the end of each matched pair of blocks (Fig. 1C).

A UV photograph of each thin section was used to identify and letter key labels that enclosed 6- or 12-mo segments of dentine. Labels and structural landmarks in the UV photograph were traced with a china marker on an overlay of transparent plastic. Using the landmarks, the tracing was lined up on the corresponding plain-light photograph onto which the labels were reproduced to delineate layering patterns within the time segments. Each marked photograph was then inspected for repeating layer components to define GLGs and their subunits in the untreated thin section. GLGs defined in the labeled dentine of each thin section were used as a basis for identifying similar GLGs in the unlabeled regions of the dentine and permitted a complete series of GLG-thickness measurements and an estimate of dentinal age in years to be made for each animal.

Dentinal GLGs in dolphin teeth are most easily discerned in the region of the "shoulder", i.e., along a transect from near the base of the neonatal line (the first layer of the postnatal dentine), downward and inward at about a 30°-40° angle to the margin of the pulp cavity (for examples see Perrin and Myrick 1980: fig. 2; Hui 1978: figs. 1, 2, 3). For consistency, measurements of GLG and label thickness, taken perpendicular to the long axis of the teeth of the Hawaiian spinner dolphins, were made along transects at a similar position and angle (Figs. 1A, B). However, a GLG or label may vary in thickness in localized regions of the dentine and may not be the same on both sides of a tooth because of tooth asymmetry. For these reasons, measurements were made on the most symmetrical side of a tooth and in regions where GLGs and labels were clearest and least variable in thickness; departing slightly from a uniform angle of transect. GLGs in the dentine of the corresponding D/S thin sections were defined and counted with the aid of GLG-thickness measurements obtained from the untreated section.

Retrospective Calibration of Cemental GLGs

Because fewer labels were observed in the cementum than in the dentine of the same untreated thin section, it was assumed that those visible represented condensed forms of only the brightest, thickest, or closely spaced groups of dentinal labels. This has been verified in bottlenose dolphins (Myrick 1980b) and recently in the present sample of Hawaiian spinners by observations that bright dentinal labels at the tooth base are continuous with cemental labels. Hence, cemental labels were lettered to correspond to the brightest dentinal labels, and the cemental layers between labels were calibrated using the time segments represented between the dentinal labels.

The annual GLG pattern was defined as precisely as possible using the calibrated segments of the tissue, and the cemental GLG definition was tested by comparing the dentinal GLG count with the cemental GLG count in untreated thin sections. In D/S thin

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[7] A commercial rapid decalcifying agent available through Dupage Kinetic Laboratories, Inc., Plainfield, Ill.

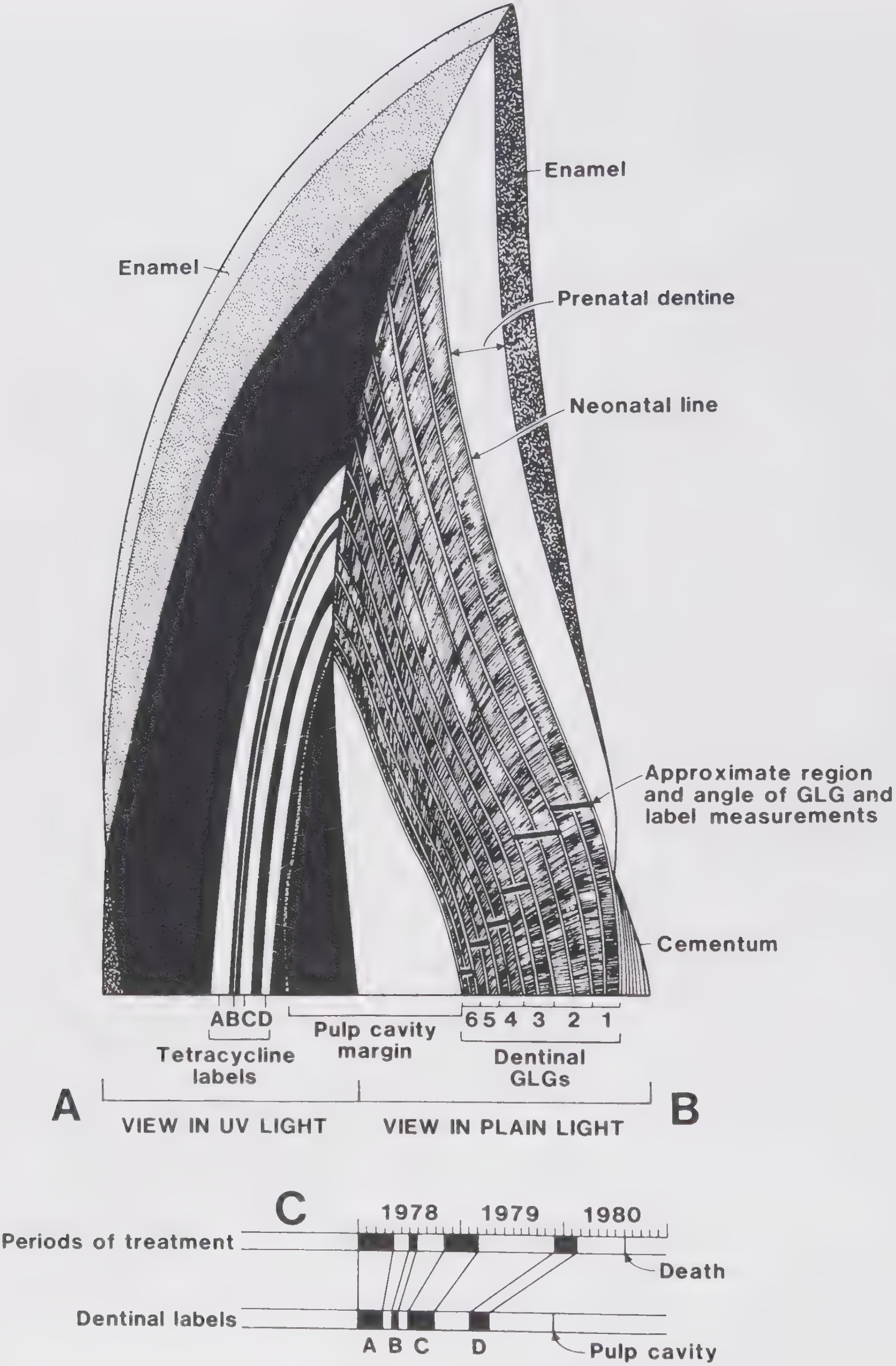
Enamel
Enamel
Prenatal dentine
Neonatal line
Approximate region and angle of GLG and label measurements
Cementum
ABCD
Tetracycline labels
Pulp cavity margin
6 5 4 3 2 1
Dentinal GLGs
A
B
VIEW IN UV LIGHT
VIEW IN PLAIN LIGHT
C
1978
1979
1980
Periods of treatment
Death
Dentinal labels
A B C
D
Pulp cavity

FIGURE 1.—Line drawing of hypothetical dolphin tooth in thin section showing appearance of TCL labels, A, B, C, D, under ultraviolet light (1A, left-hand side) and dentinal growth layer group (GLG) layering patterns under plain transmitted light (1B, right-hand side), and standard positions in tooth where label and GLG thickness are measured. 1C illustrates method of identifying labels in tooth section with TCL treatment dates by comparing relative thickness and spacing of labels with treatment periods.

sections, cemental GLGs were defined indirectly by comparing them with the pattern and number of cemental GLGs determined in untreated sections.

Direct Monitoring

Calculation of depositional rates and calibration and definition of GLGs in dentine and cementum were achieved by comparing tooth specimens containing successively introduced labels and/or additional tissue accumulated over the 1-yr period of monitoring. To make determinations, for cases in which labels were not distinct or not successfully produced, the additional tissue was measured from structural landmarks or labels in the extracted series of thin sections.

RESULTS

Dentinal labels.—The untreated thin sections for all seven specimens contained multiple labels. Most attempts to match labels with treatments were successful (Figs. 2-6). However, in four specimens more labels occurred than could be accounted for from clinical records. In the only captive-born specimen, WFP 670, numerous TCL labels were observed (Fig. 7A, B), but only three were found to have been caused by intentional therapeutic treatments (Fig. 7D, labels C, F, and G). Labels A and B apparently were a result of TCL impa~~ir~~rted to the then-calf through the milk of its mother, who was treated with the drug for two periods while the calf nursed. The other labels appear to have resulted from frequent ingestion of stolen TCL-dosed smelt intended for other dolphins being treated at various times while sharing a common tank with this animal.

No treatment was recorded for label A found in the dentine of dolphin carcass WFP 669 (Fig. 4A, C) and live dolphin ACM 104 (Fig. 6A, C). Judging from the relative positions of the "A" labels to the other labels for which matches were found with recorded treatments, "A" labels were introduced into both specimens at or about their respective dates of capture. It is a fairly common practice in commercial aquaria to give medication (often tetracycline) to newly captured dolphins recovering from stress of capture and adjusting to the captive environment[8].

Labels B and G in the dentine of dolphin carcass WFP 671 could not be identified from clinical records (Fig. 5A, C), although the numerous other labels match well in relative thickness and spacing with the treatment dates for this specimen.

In teeth of live dolphin ACM 103 the labels were indistinct. The presence of TCL, introduced clinically during three periods of treatment over 2 yr and experimentally at 3-mo intervals in 1980, was indicated only by several areas of hazy fluorescence in the dentine near the pulp cavity.

Dentinal GLG pattern.—The use of plastic overlays of key labels enclosing 6-mo or 1-yr segments of dentine on plain-light photographs of the dentine for each specimen permitted repeated calibrations of the annual dentinal layering pattern for six of the seven specimens (the seventh specimen, ACM 103, had no discrete labels). In untreated thin sections, a dentinal GLG contained four major components deposited in the following sequence: 1) A thin, light (GLG-boundary) layer, 2) a thicker dark layer, 3) another thin, light (mid-GLG) layer, and 4) a second thick, dark layer (Figs. 3A, 4B, 5B, 6B).

In addition to the four components, many of the earliest deposited GLGs had an infrastructure composed of finer alternating dark and light layers. Counts made at 150× under low transmitted light showed that each of these annual GLGs contained 13 pairs of fine layers (Figs. 3A, 4B, 6D, 7C). Where layers were sufficiently distinct to be counted between labels (e.g., between label B and M, Fig. 4A, B), counts indicated that each pair ["LML," (lunar monthly layer) Myrick 1980b] represented about 1 lunar month. The full complement of LMLs was visible throughout the dentine in the captive-born specimen, WFP 670, i.e., 13 LMLs in each of the first three complete GLGs and 9 in the incomplete fourth GLG (Fig. 7C). In specimen ACM 103, 13 LMLs were observed in the first 12 of the 14.5 GLGs present (Fig. 8).But in other specimens, LMLs were clear enough to be counted only in the first five or six GLGs.

In D/S thin sections, the annual GLG pattern consisted of two lightly stained and two darkly stained layers. The thin, light, GLG-boundary layers and mid-GLG layers in untreated thin sections corresponded to the lightly stained layers in D/S thin-sections (Fig. 9A, B). LMLs were indistinct in almost all GLGs in D/S preparations.

Age-specific GLG thickness.—Table 1, showing dentinal GLG thickness measurements made from the most symmetrical side of the tooth of each of the seven dolphins, indicates that for each animal a GLG of a specific thickness was produced that appears to be related to the year of life in which the GLG was formed, i.e., an age-specific GLG thickness.

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[8] William A. Walker, Los Angeles County Museum of Natural History, Los Angeles, Calif., pers. commun. 1982.

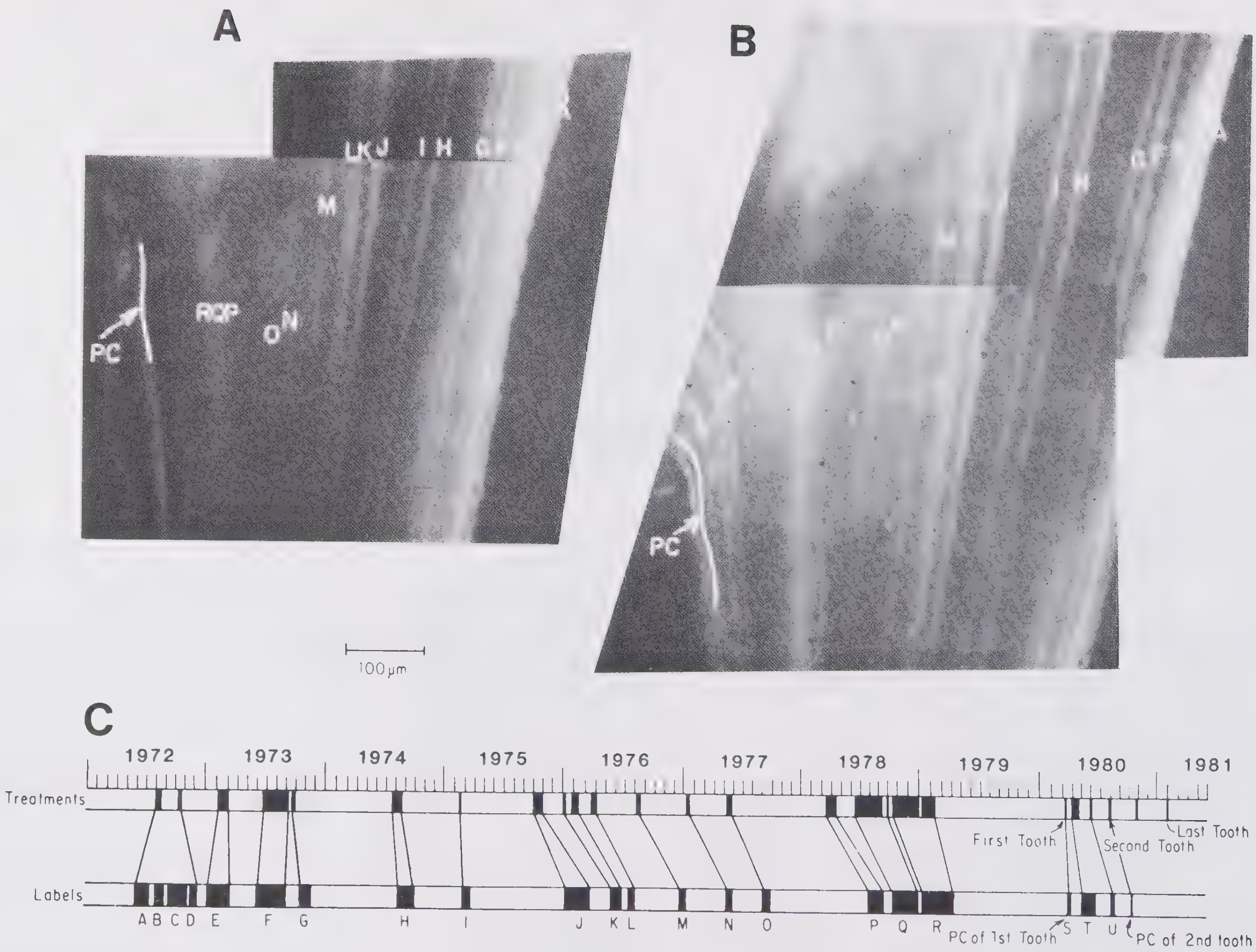
A
B
C
PC
RQP
O N
M
L K J
I H
G
PC
M
I H
G F
100 µm
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Treatments
Labels
A B C D E F G H I J K L M N O P Q R S T U
First Tooth
Second Tooth
Last Tooth
PC of 1st Tooth
PC of 2nd tooth

FIGURE 2.—Labeled teeth from live dolphin ACM 106. A. Untreated thin section of tooth extracted in March 1980, showing labels (lettered) introduced through TCL treatments from 1972 through 1979 (UV, 150×). B. Tooth extracted 4 mo after tooth in 2A showing three labels introduced during first part of the experimental labeling period. Label T was produced from a clinical treatment administered over 1-mo period (UV, 150×). C. Chart showing treatments and corresponding dentinal labels as interpreted from relative label positions and thicknesses.

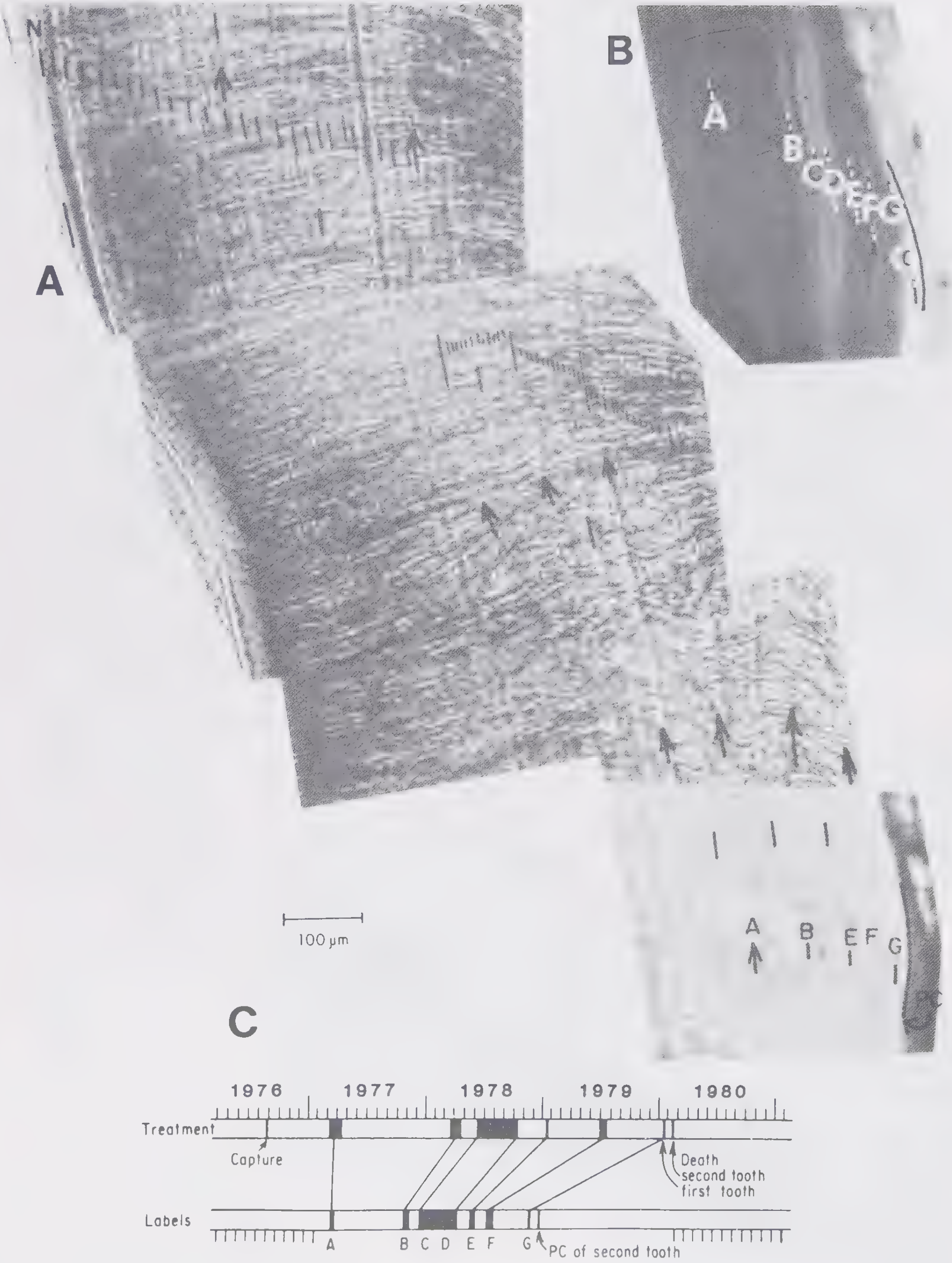
A
N
B
A
B
C
D
E
F
G
C
100 μm
A
B
E
F
G
C
1976
1977
1978
1979
1980
Treatment
Capture
Death
second tooth
first tooth
Labels
A
B
C
D
E
F
G
PC of second tooth

FIGURE 3.—Labeled tooth taken from dolphin carcass WFP 606. A. Untreated thin section in plain light showing about eight annual GLGs in dentine (separated by arrows). GLGs divided approximately in half by thin, light mid-GLG layers (heavy dark marks). GLGs 6, 7, and 8 were interpreted from positions of tetracycline labels (lettered). Finer dark layers represent lunar monthly layers (150×). B. Dentine labels in UV light (150×). C. Chart showing dates labels were introduced.

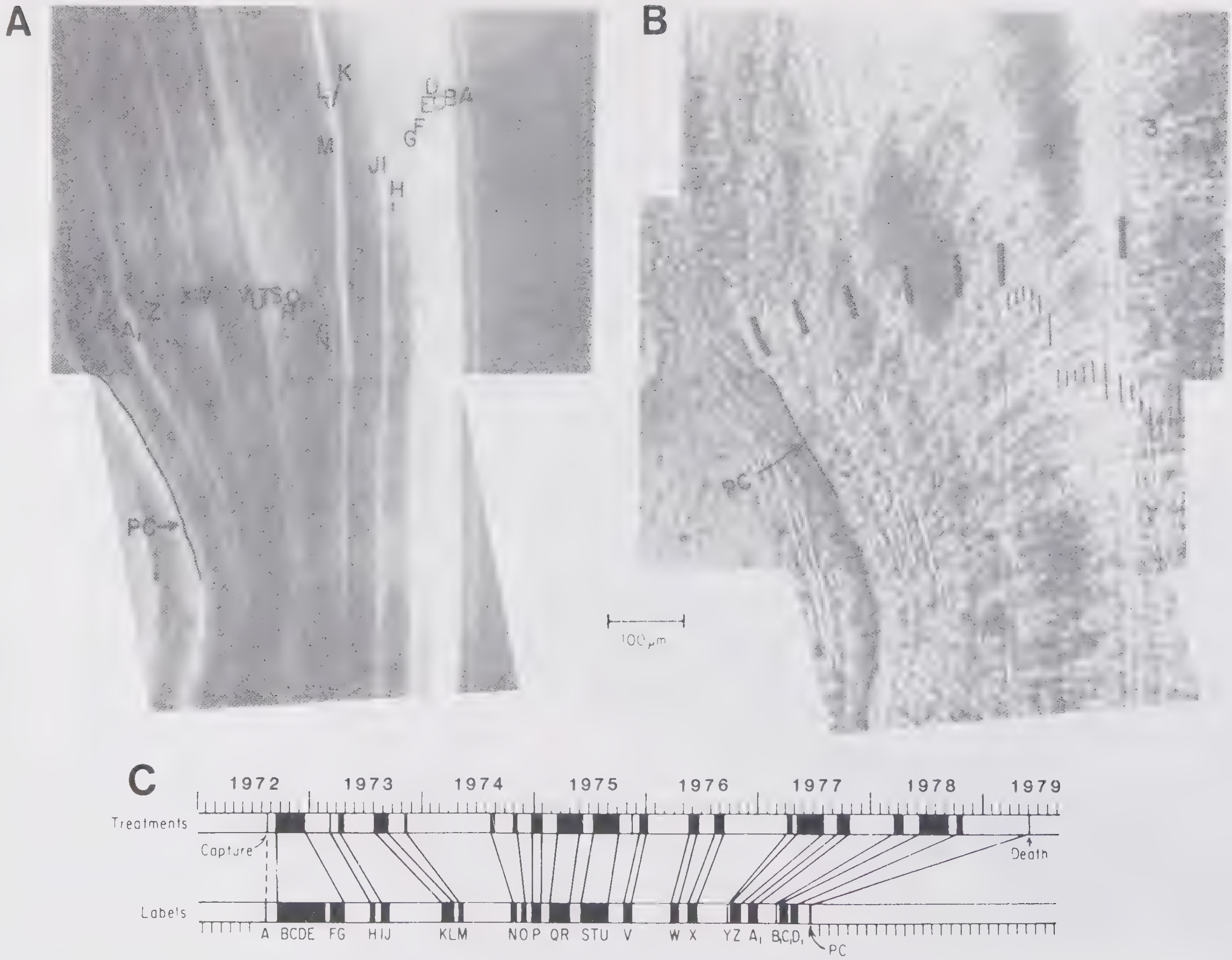
A
K
L
M
D
C
B
A
E
F
G
J
I
H
Z
A1
X
W
V
U
T
S
Q
R
P
O
N
PC
B
3
PC
100 μm
C
1972
1973
1974
1975
1976
1977
1978
1979
Treatments
Capture
Death
Labels
A
BCDE
FG
HIJ
KLM
NOP
QR
STU
V
W
X
YZ
A1
B1C1D1
PC

FIGURE 4.—Labeled tooth from dolphin carcass WFP 669. A. TCL labels (lettered) in region of dentine pulp cavity (PC) (UV, 150×). B. Plain-light view of dentine as in 3A showing annual GLGs bordered by light boundary layers (heavy dark marks) as interpreted from key TCL labels. Fine dark lines represent LMLs. (Heavy lines delineating GLGs are not placed at the standard positions used to measure GLG and label thickness.) C. Chart showing TCL treatments and corresponding dentinal labels identified by comparing relative positions and thicknesses of labels with spacing of treatment blocks.

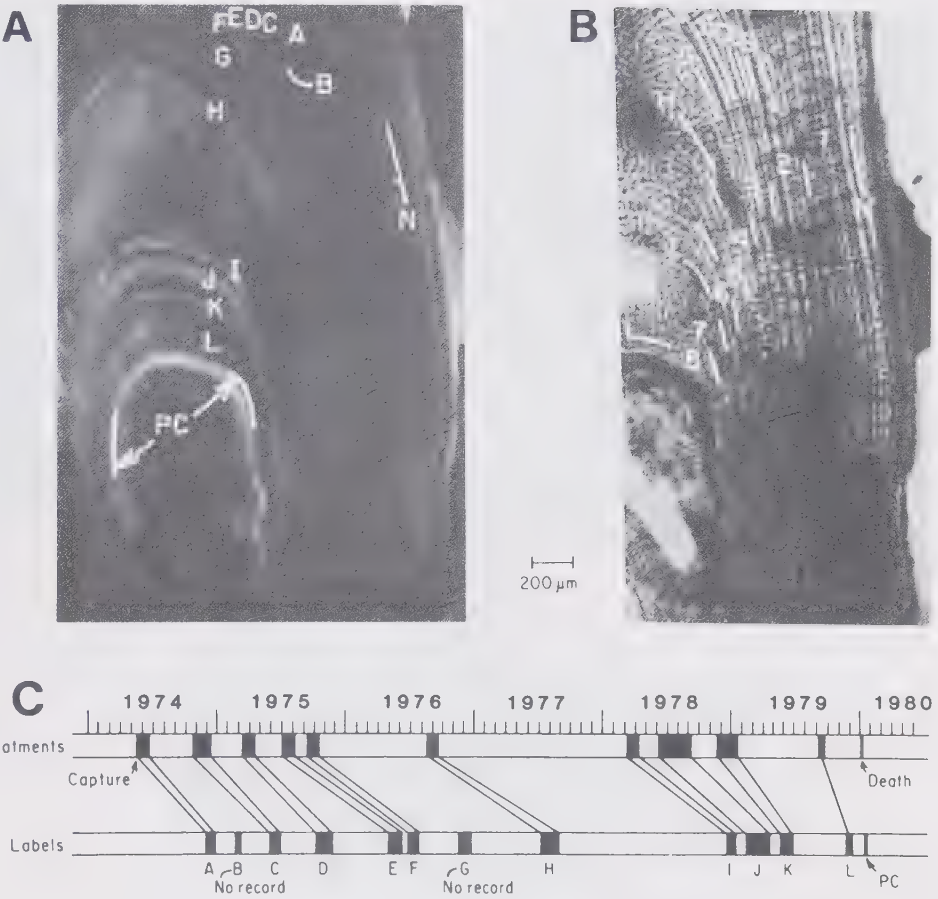

FIGURE 5.—Labeled tooth of dolphin carcass WFP 671. A. Untreated thin section in UV light showing TCL labels (39×). B. Thin section in plain light showing almost eight complete GLGs as interpreted from labels. Light GLG boundary layers appear to have been deposited in or about March (39×). C. Chart showing match between labels and treatments.

TABLE 1.—Mean age-specific thicknesses (µm) of completed dentinal growth layer groups (GLGs) in teeth of seven Hawaiian spinner dolphins, *Stenella longirostris*. Values are averages of at least three measurements per specimen, taken perpendicular to the long axis of the tooth in a stairstep fashion downward and inward from the base of the neonatal line to the pulp-cavity wall.

Specimen	GLG number														
no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
WFP 670	240	240	180	—	—	—	—	—	—	—	—	—	—	—	—
WFP 669[1]	240	240	172.5	150	127.5	127.5	92.5	85	65	57.5			—		—
WFP 671	240	240	165	140	120	95	80	—	—	—	—	—	—	—	—
ACM 104	240	230	170	140	130	90	90	70	70	60	55	—	—	—	
ACM 103	240	240	180	160	110	80	80	70	60	60	60	65	55	40	40
ACM 106	240	240	150	130	110	90	90	60	60	60	55	–			—
WFP 606	240	240	180	150	120	90	90	—	—	—		—			—
N	7	7	7	6	6	6	6	4	4	4	3	1	1	1	1
$\bar{x}$	—	238.6	171.0	145.0	119.6	95.4	87.0	71.3	61.3	58.1	55.0	—	—	—	—
SD	—	3.8	11.0	10.5	8.4	16.5	5.6	10.3	2.5	2.4	5.0	—	—	—	—
SE	—	1.4	4.2	4.3	3.4	6.7	2.3	5.2	1.3	1.2	2.9	—	—	—	—

[1] Mean values of measurements in untreated and D S (decalcified and haematoxylin-stained) sections.

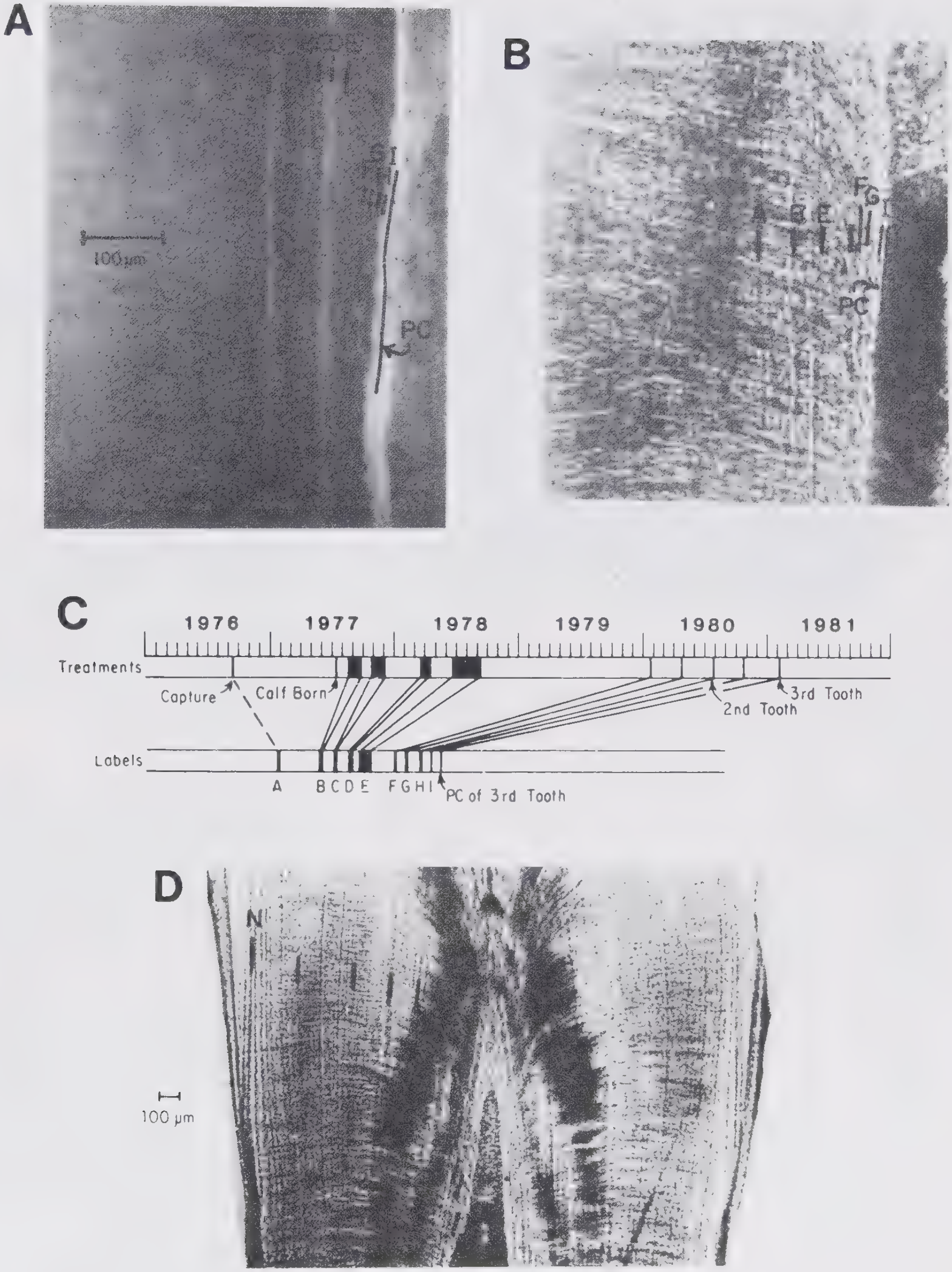
A
100µm
S I
PC
B
A
B E
FG I
PC
C
1976
1977
1978
1979
1980
1981
Treatments
Capture
Calf Born
2nd Tooth
3rd Tooth
Labels
A
B C D E
F G H I
PC of 3rd Tooth
D
N
100 µm

FIGURE 6.—Tooth of live dolphin ACM 104 extracted 2 February 1981. A. Untreated thin section in UV light showing location of TCL labels (150×). B. Same section as in 6A in plain light showing position of key labels bracketing last 4 yr of deposition. Light GLG boundary layers appear to have been deposited in or about August. C. Chart showing match of labels and treatments. D. Thin section showing 11 complete annual GLGs (separated by dark marks) as interpreted from labels (39×).

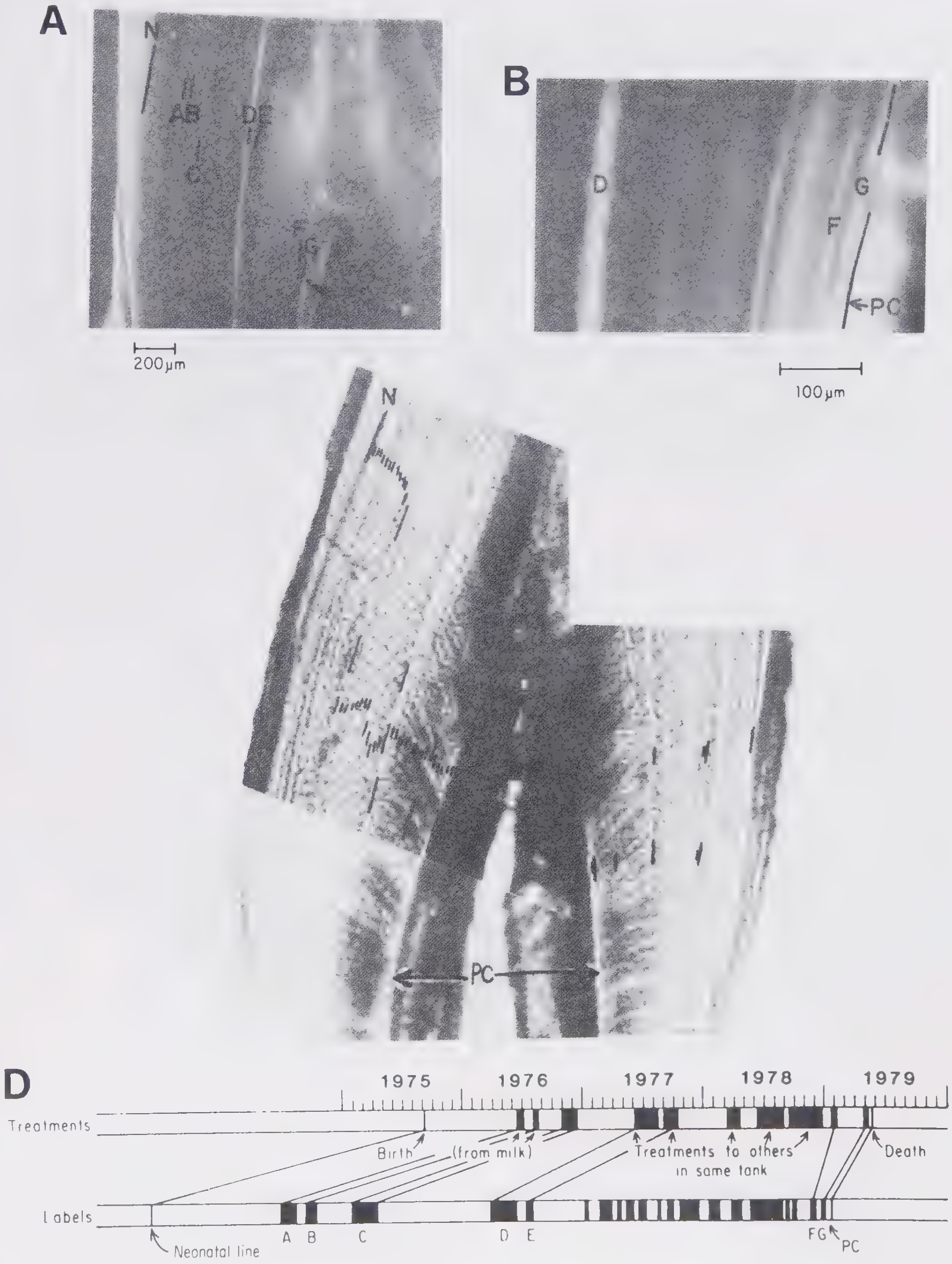
A
N
AB
DE
C
F
G
200µm
B
D
G
F
PC
100µm
N
PC
D
1975
1976
1977
1978
1979
Treatments
Birth
(from milk)
Treatments to others
in same tank
Death
Labels
Neonatal line
A
B
C
D
E
FG
PC

FIGURE 7.—Teeth from dolphin carcass WFP 670 (captive-born animal). A. Untreated thin section showing TCL labels in dentine. Labels A-B apparently represent TCL imparted to this animal through its mother's milk (UV, 39×). N = neonatal line; PC = pulp cavity margin. B. Portion as shown in 1A showing numerous labels from TCL-dosed smelt stolen from other dolphins occupying the same tank. Labels F and G represent direct treatments administered shortly before death (UV, 150×). C. Thin-sectioned tooth showing three entire and one partial GLGs (indicated by heavy dark marks) in the postnatal dentine as interpreted from TCL labels. LMLs are indicated by fine dark markers (plain transmitted light, 150×). D. Chart showing dates of direct and presumed incidental introduction of TCL and corresponding labels identified in the dentine by relative label position and thickness.

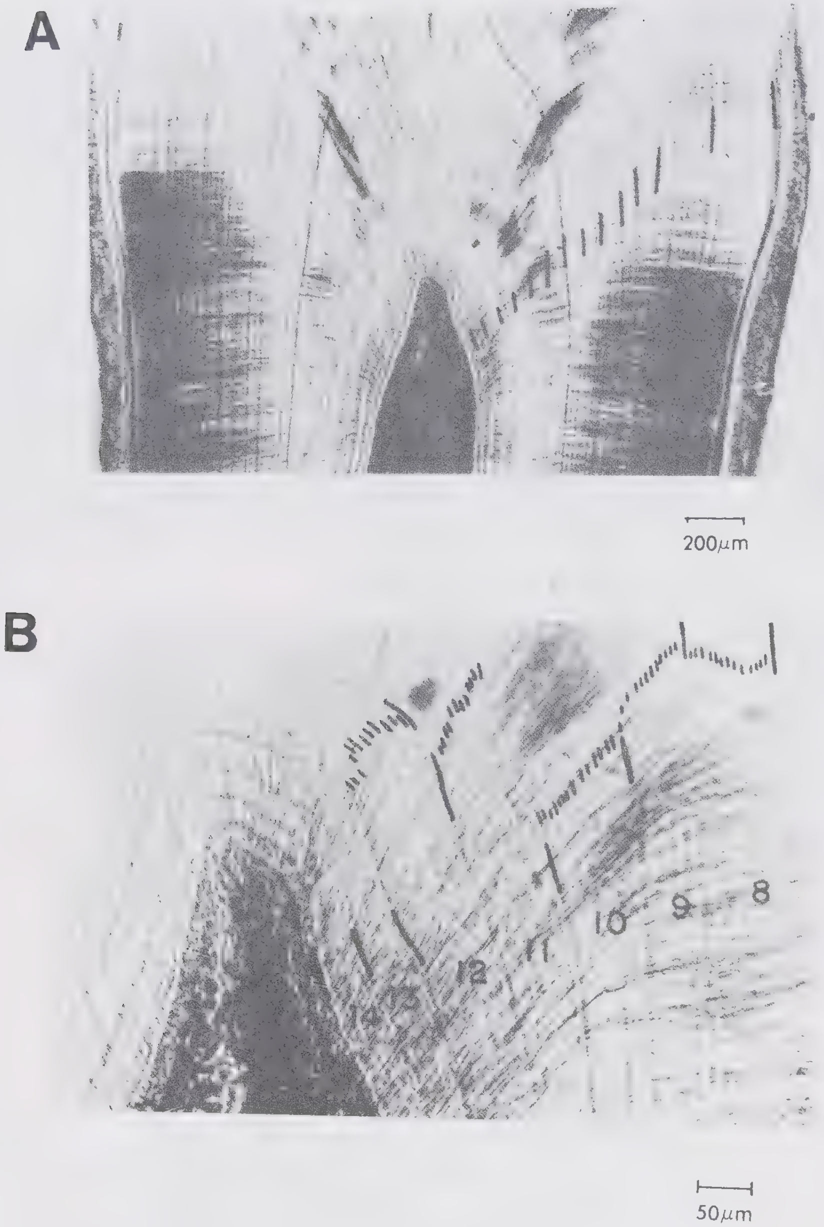

FIGURE 8.—Untreated tooth of live dolphin ACM 103 extracted 25 January 1980. A. About 14½GLGs indicated (heavy dark marks) (39×). B. GLGs 8-14½ showing thin, light boundary layers with dark margins. Thirteen LMLs indicated in each GLG 8-12 are particularly well developed (150×).

Comparisons of age-specific GLG thickness among the specimens suggest that the animals deposited a GLG of similar thickness in the same year of life. In the first and second year, 240 μm thick GLGs were deposited. In the third, fourth, fifth, sixth, and seventh years, thickness of GLGs averaged 171, 145, 119, 95, and 87 μm respectively. From the 8th to the 11th year, GLGs were between 71 and 55 μm thick. The data in Table 1 represent averages of at least three measurements per GLG per specimen.

Cemental labels.—Relatively few TCL labels were

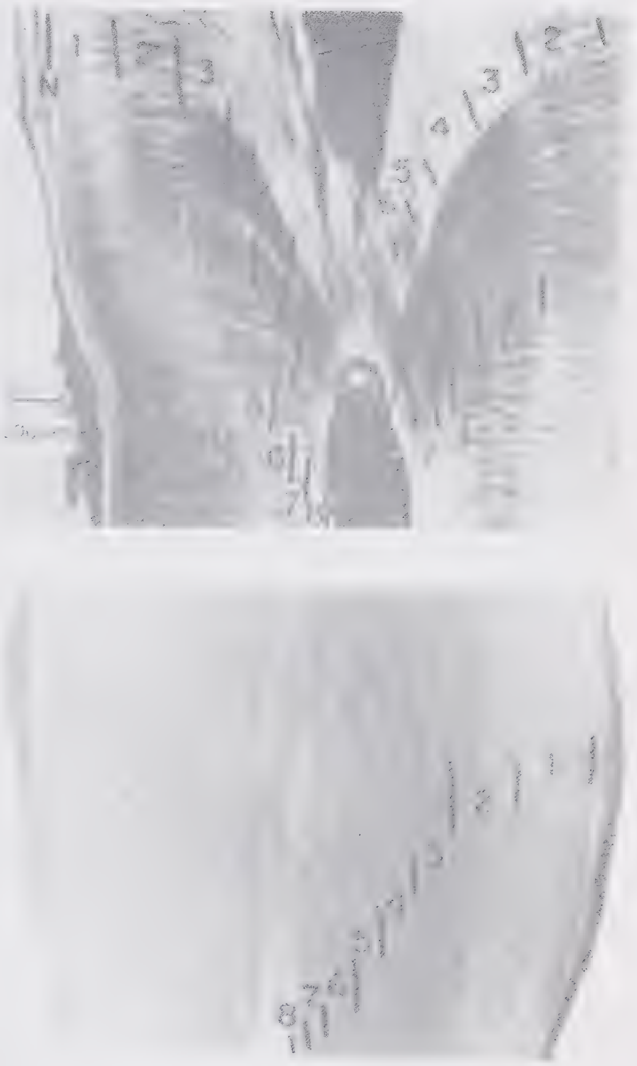

FIGURE 9.—Comparison of GLG patterns in teeth from dolphin carcass WFP 606 prepared by two methods: A. Untreated thin section (39×). B. Decalcified and stained thin section (39×).

found in the cementum compared with those in the dentine of the specimens. In the captive-born specimen, WFP 670, with about 25 dentinal labels, the cementum contained only three labels. In specimen WFP 669, only four cemental labels were observed (Fig. 10A) compared with 30 dentinal labels (Fig. 4A). The cementum in the other specimens had either zero or 1 label, despite the numerous dentinal labels observed for each.

Cemental GLG pattern.—In untreated thin sections, a cemental GLG consisted of a dark layer and a light layer (Fig. 10B). In D/S sections it was composed of a dark-stained layer, corresponding to the dark layer in untreated sections, and a lightly stained layer (Fig. 11). In both types of preparations, the dark layers contained larger concentrations of cementocytes than did the light layers.

Calibration of cemental GLGs.—Calibrations of cemental GLGs with those in the dentine were carried out using the assumption that cementum is a less sensitive recording structure than dentine (Klevezal' 1980) and that labels occurring in the cementum corresponded only to the brightest and thickest labels or label groups in the dentine. Thus, for example, the four labels detected in the cementum of specimen WFP 669 (Fig. 10A) were flagged with the same letters used to identify multiple label concentrations in the dentine (Fig. 4A).

In some cases, such as in WFP 669, plastic overlays were used to determine that a cemental GLG rep-

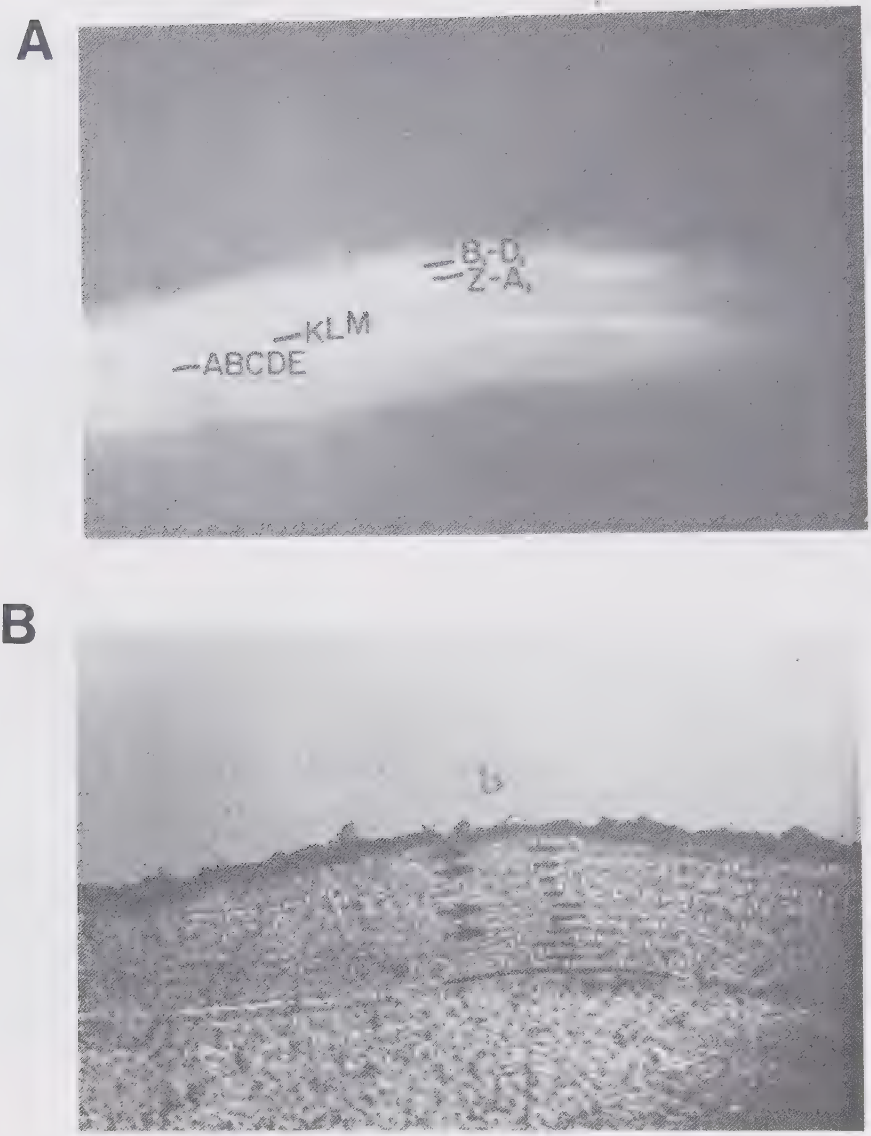

FIGURE 10.—Tooth cementum of dolphin carcass WFP 669. A. TCL labels interpreted as corresponding to lettered dentinal labels (150×). B. Positions of TCL labels (arrows) in layered cement. About 10 GLGs are indicated (150×).

resented the same amount of time as a dentinal GLG, i.e., 1 yr (e.g., Fig. 10B). In other cases, where labels were absent or where only one label occurred, calibration of cemental GLGs with dentinal GLGs was made indirectly by comparing GLG counts from both tissues. This method usually demonstrated a one-to-one relationship of GLGs in dentine and cementum, but in a few regions of the cementum of the captive-born specimen, WFP 670, there were twice as many GLGs as in the dentine (Fig. 11), indicating that a GLG may have been deposited twice a year in the cementum. In expanded regions of the cementum in another specimen (ACM 104; see Table 2), the cemental count was equal to the dentinal count; but in thinner regions the cemental count was only half that of the dentine, suggesting a cemental GLG being deposited every 2 yr in some cases.

Direct monitoring.—The results of examinations of thin sections of the series of three teeth from each of three live animals, taken at the beginning, at mid-point, and at the end of a 1-yr monitored period are

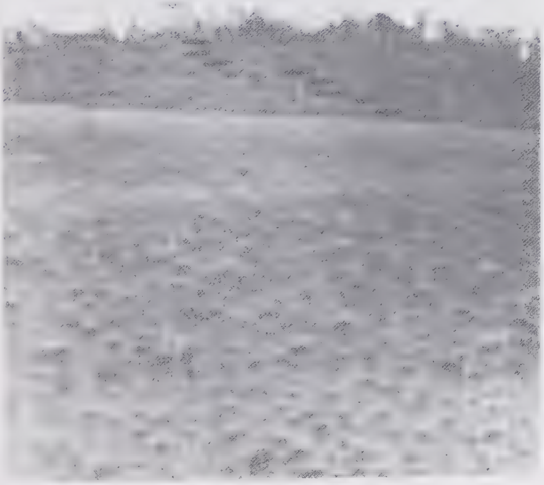

FIGURE 11.—Cementum of dolphin carcass WFP 670 tooth in decalcified and stained thin section. The number of dark layers is eight, about double the age in years of this captive-born specimen (150×, plain transmitted light).

presented in Table 2. Although distinct labels were not always successfully introduced, dentinal and cemental GLGs continued to be accumulated at a uniform rate of one per year. A comparison of accumulated dentine and labels in the first two extracted teeth of specimen ACM 106 (Fig. 12) showed two experimental treatments and one (unscheduled) clinical treatment accounted for in the second tooth (Fig. 2A-C). Specimen ACM 103, in which premonitor labels were indistinct, showed no experimental labels but clearly showed continued accumulation of dentine, the third extracted tooth having added about one GLG over the 1-yr period. No experimentally introduced labels were observed in the (less sensitive) cementum in any teeth of the three animals, but cemental deposition of about one complete GLG occurred in each animal for the period.

Seasons of birth.—By determining the dates of key dentinal labels introduced at or near the thin, light component layers of GLGs and by noting the approximate time of formulation of component layers in the teeth extracted during the monitor period, it was found that GLG-boundary and mid-GLG layers were formed at about 6 mo intervals. In five specimens, GLG-boundary layers were deposited in or about August and the mid-GLG layers were deposited in or about March. In the two other specimens the timing was reversed, i.e., GLG-boundary layers formed in March, mid-GLG layers in or near August. Proceeding on the assumption that the timing of layer formation (determined from the labeled or monitored

TABLE 2.—Results of examinations of teeth extracted from three live Hawaiian spinner dolphins, *Stenella longirostris*, over a 1-yr period monitoring accumulation of layers and labels. GLGs = growth layer groups.

Specimen no. and tooth	Date of tooth extraction	Date label introduced	Dentine		Cementum	
			Additional labels	No. GLGs	Additional labels	No. GLGs
ACM 103						
First	25 Jan 1980	25 Jan 1980 30 Apr 1980	—	14.5	—	14.5
Second	30 July 1980	30 July 1980 30 Nov 1980	indistinct	15.0	None	15.0
Third	2 Feb 1981	—	indistinct	15.5	None	15.5
ACM 106						
First	19 Mar 1980	19 Mar. 1980 11-28 Apr 1980[1] 5 June 1980	—	10.3	—	10
Second	30 July 1980	30 July 1980 30 Nov 1980	3	10.7	None	10+
Third	2 Feb. 1981	—	indistinct	11.2	None	11
ACM 104						
First	25 Jan. 1980	25 Jan. 1980 30 Apr 1980	—	([2])	—	([2])
Second	30 July 1980	30 July 1980 30 Nov 1980	2	10.7	None	[3]5/10
Third	2 Feb 1981	—	4	11.3	None	[3]6/11

[1] Unscheduled medical treatment 18 d in duration

[2] Not examined because of poor preparation of section

[3] Cementum showed a number of GLGs equal to that of the dentine as well as half that of the dentine

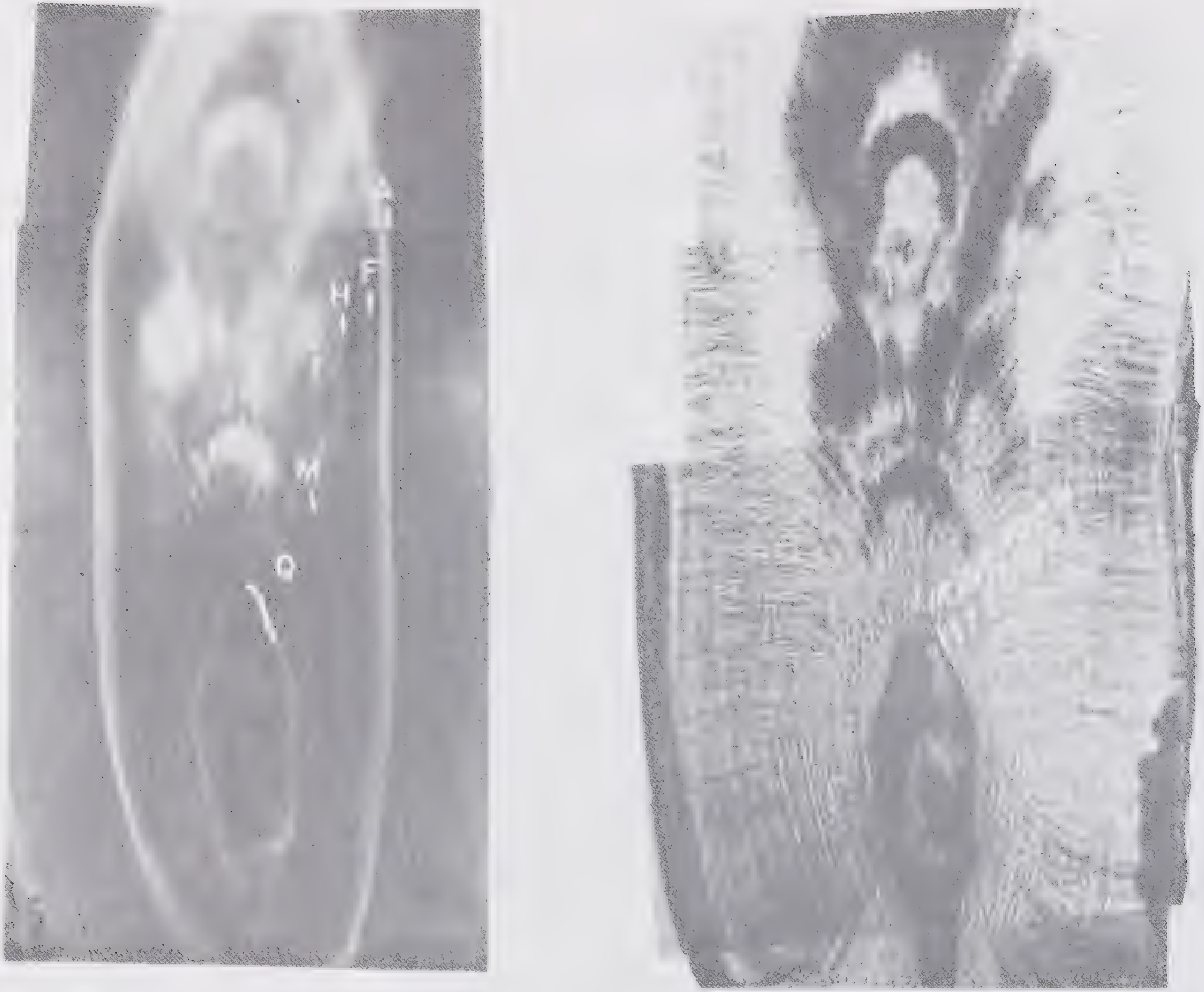

FIGURE 12.—Tooth of live dolphin ACM 106 extracted 30 July 1980. A. Untreated thin section in UV light showing key labels A-M each introduced 1 yr apart, M and Q 2 yr apart, and almost 1 yr of dentine accumulation represented between Q and the pulp-cavity margin (39×). B. Thin section as in 12A (plain light) showing GLGs as interpreted from labels. Positions of labels A and F are indicated. Horizontal white lines indicate positions and angle of transect. GLG thickness measurements were taken for GLGs 1-3.

regions of the dentine) was uniform throughout all of the dentine for a given specimen, GLG-boundary and mid-GLG layers were counted in reverse order of deposition up to the first boundary layer, the neonatal line, to estimate month and year of birth.

Table 3 summarizes the month- and year-of-birth estimates made from boundary-layer counts in six specimens and birth dates taken from park records of two captive-born specimens, WFP 670 and the calf of ACM 104. Six were born in late summer/early autumn and two in March.

TABLE 3.—Estimated birthdates of eight captive Hawaiian spinner dolphins, *Stenella longirostris*..

Specimen no.	Month and year of birth
ACM 103	August 1964
ACM 106	August 1969
WFP 669	August 1969
ACM 104	September 1969
WFP 606	March 1972
WFP 671	March 1973
WFP 670[1]	8 September 1975
Calf of ACM 104[2]	21 July 1977

[1] Born in captivity

[2] Born in captivity, survived 3 d

DISCUSSION

Age-Specific GLG Thickness

Dentinal GLG thickness appears to be age-specific for the Hawaiian spinner dolphin teeth examined. There was little variability from tooth to tooth or from animal to animal in the sequence of GLG thickness through the 11th GLG, despite deposition of a specific GLG in some specimens while still in the wild and in other specimens during their captive lives. This suggests that, to some extent at least, the amount of dentine deposited by animals at a given age may be predetermined and that animals of a given stock, species, or higher common phylogenetic affinity may follow the same or similar pattern of age-specific GLG deposition unaffected by environment.

Used in conjunction with the GLG component-layer pattern, the regularity in thickness of age-specific GLGs may be useful as an aid in locating GLG boundaries and counting GLGs in teeth of wild Hawaiian spinner dolphins and dolphins of related species in which GLG thickness and component-layer patterns are found to be similar. When measurements are taken at standard positions in the teeth of such dolphins, one may make fairly rapid age estimates without having to examine each GLG in detail (see Myrick et al. 1983).

Lunar Monthly Layers (LMLs)

Laws (1962) was the first to suggest that the system of fine layers within dentinal GLGs of pinniped teeth corresponded to lunar monthly cycles. Putative LMLs have been reported in dentine of dugongs (Kasuya and Nishiwaki 1978; Marsh 1980), in dentine of beaked whales ("short cycles," Kasuya 1977; "accessory layers," Perrin and Myrick 1980:3, 5), in fossil dolphin teeth (Myrick 1979), and in the mandibular bone (Myrick 1980b) and dentine of modern dolphins (Myrick 1980b; Hohn 1980a, b). Hui (1978) reported finding no relationship between the fine layers that he counted in a tooth from a known-age bottlenose dolphin and its age in lunar months; but with no prior knowledge of its age, Myrick (1980b) made dentinal LML counts in the same specimen that closely agreed with its known age.

The present study has furnished verification that LMLs are deposited with lunar-monthly regularity in the animals studied. In the 3.7-yr-old captive-born spinner dolphin (WFP 670), 13 LMLs were counted in each of the three complete annual dentinal GLGs and 9 were counted in the partial fourth GLG. Where LMLs were visible between TCL labels in the dentine in this and other specimens, they were found to correspond consistently in number to the time in months represented between labeling dates.

Where LMLs could be seen clearly, no departure from the 13 LML/GLG pattern was detected in the teeth used in the present study. Variability has been reported in studies of other marine mammals. Marsh (1980:197) found only "about 12 [LMLs] per GLG" in the dentine of the deciduous incisor of a dugong. Ten to 15 LMLs/GLG were observed in dugong tusks by Kasuya and Nishiwaki (1978). Kasuya (1977) found between 11 and 13.4 LMLs ("short cycles")/GLG in teeth of Baird's beaked whales, *Berardius bairdii*. Hohn (1980b) counted 10-13 LMLs/dentinal GLG in Atlantic bottlenose dolphin teeth. Presumably, LML variability will be found to occur also in Hawaiian spinner dolphins when larger samples are examined.

Relationship of Cemental GLGs to Dentinal GLGs

None of the teeth of the studied specimens had reached the stage of pulp-cavity occlusion or dentinal irregularity that necessitated age estimation solely from cemental GLG counts (Kasuya 1976; Myrick et al. 1983). Although the pulp cavities were small in some specimens and some later-administered TCL failed to produce distinct labels, none showed evidence of cessation of dentine deposition.

All cemental GLG counts corresponded in number to dentinal annual GLG counts except in the case of specimen WFP 670, where some regions of the cementum showed double the number, and in specimen ACM 104, where in some places the cemental count was half that of the dentine. The finding that in some cases cemental GLGs may form at half or twice the rate of dentinal GLG deposition points up the problem of using cemental GLGs to estimate ages without reference to the dentine (Myrick et al. 1983).

Evidence for an Internal Clock

In the dentine of the animals studied, a thin GLG boundary layer, beginning with the neonatal line, was formed in the month of birth and on anniversaries of the month of birth. Mid-GLG layers were formed about 6 mo after formation of boundary layers. Where LMLs could be calibrated, one was found to form about every (lunar) month with high uniformity in relative spacing. Such a cycle of deposition is indicative of an internal clock, or clocks. The pattern commences at birth and apparently is reset with solar and/or lunar regularity without perceptible alteration by fluctuation in the dolphins' natural or captive environment or in calendric season of birth. That it may not be a totally free-running system, i.e., not without external cues, is suggested by the precisely synchorized deposition of the fine and coarse patterns of the dentine repeated over many years.

Age at Sexual Maturity

Perrin et al. (1977) indicated that sexual maturity may be reached in females of *Stenella longirostris* at an average 5.5 yr (range of 5-9 yr) and the average period of gestation may be about 11 mo. From the study of dentinal GLGs and TCL labels of specimen ACM 104, it was possible to determine that this animal was about 8-yr-old when she gave birth to her calf. Assuming an 11-mo gestation, we estimate that she would have been 7-yr-old when she conceived. It is not known whether the pregnancy resulted from fertilization at her first or subsequent ovulations. ACM 104 remains alive. This precludes examination of her ovaries for ovulation scars.

Reproductive Seasonality

Based on the birth records of specimen WFP 670 and the calf of ACM 104 and the deductions made from dentinal layers, six animals were born in late summer/early fall, and two were born in March. Since all animals in the study represented the same population off Kona, Hawaii, the early-spring and early-fall birth patterns might indicate a corresponding two-cycle pattern of reproductive peaks for the wild population generally. Such a seasonal pattern has been suggested by Norris and Dohl (1980, fig. 16), but Wells (in press), who has studied the population in considerable detail, concluded that the breeding season occurs from spring to fall, with most births in the fall. Our sample was too small to verify Wells' findings.

Tetracycline Exposure to the Calf Through the Milk

The first two labels found in the dentine of specimen WFP 670, the captive-born animal, were interpreted as having been introduced through milk received by the calf while the mother was being treated with TCL. This recommends a possible practical application in indirectly treating newborns in ill health. Excessive handling of such animals frequently results in a worsening of their condition, making the treatment more dangerous than the malady. (Nursing calves not on solid food cannot be treated with TCL-dosed fish and must be force-fed or injected with drugs.) Separating the young calf from its mother may produce additional complications.[9] If treatments for the calf could be administered through the milk by treating the mother with TCL-dosed food, it seems likely that most of the problem could be minimized. The question invites further study.

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8464

Myctophidae: Relationships

J. R. Paxton, E. H. Ahlstrom and H. G. Moser

THE family Myctophidae has usually been placed in the order Myctophiformes (Iniomi, Scopeliformes) since the work of Regan (1911a), who recognized two suborders, the Myctophoidea and Alepisauroidea (ateleopodids, given a third suborder, are currently placed elsewhere). The families Myctophidae and Neoscopelidae have long been considered close relatives; they were placed in one family until 1949 (Smith). Although Greenwood et al. (1966:371) relegated the order to a subordinal level within the Salmoniformes, they pointed out that myctophoids, and neoscopelids in particular, possess advanced characters that indicate they may be ancestral to the paracanthopterygian radiation. Paxton (1972:54–55) considered myctophids and neoscopelids most closely related to the Chlorophthalmidae, with that evolutionary line of the Myctophoidea arising from an aulopid-like ancestor. Moser and Ahlstrom (1970:141–142) described the larval similarities in the families Chlorophthalmidae, Neoscopelidae and Myctophidae.

Family Relationships

Rosen (1973, 1982) split off the Myctophidae and Neoscopelidae as a restricted order Myctophiformes which he considered the primitive sister group of both the Paracanthopterygii and Acanthopterygii; the remaining myctophiform families were placed in a new order Aulopiformes. Matsuoka and Iwai (1983) found cartilage in the adipose fin of only the Myctophidae and Neoscopelidae in the five 'iniomous' families they studied. Okiyama (1974b) studied the relationships of the suborder Myctophoidea (*sensu* Gosline et al., 1966) and based on larval peritoneal pigment spots and the relationship of abdominal to caudal vertebrae, three familial groups were recognized: Aulopidae-Synodontidae-Bathysauridae, Chlorophthalmidae-Ipnopidae and Neoscopelidae-Myctophidae. Sulak (1977) lumped the Ipnopidae and Bathypteroidae into the Chlorophthalmidae and the Harpadontidae and Bathysauridae into the Synodontidae, considering both groups arose from the Aulopidae; he did not consider the position of the Myctophidae. Schwarzhans (1978) considered myctophids and neoscopelids most closely related and distinct from Aulopiformes on the basis of otolith morphology.

In his excellent study of the Evermannellidae, Johnson (1982) presented a rigorous analysis of 51 characters involving mostly adult but some larval features. He concluded that neoscopelids and myctophids are most closely related to each other, sharing eight derived character states, but that they were the sister group of four families (Notosudidae, Scopelarchidae, Chlorophthalmidae and Ipnopidae) constituting a chlorophthalmoid group within the Myctophiformes. However, he noted only a single shared derived character in those six families, and it is shared with part of another line. Johnson (1982:95) placed the Aulopidae in a second line and all remaining families in the third

TABLE 63. CHARACTERS OF THE MYCTOPHIDAE. (0) = plesiomorphic state, (1) = apomorphic state, (2) = different or advanced apomorphic state, 1 = by outgroup comparison, 2 = raised photophore, 3 = generalized larva, * = discussed in text.

Characters

1. Jaws long (0), moderate (1), short (2)—*.
2. Extrascapulars 2 (0), 1 from fusion (1), 1 from loss (2)—*.
3. Cleithral shelf absent (0), present (1)—1.
4. Prc 3–9 (0?), 1–2 (1?)—*.
5. Larval eyes round (0), narrow (1)—1, 3.
6. Dn present (0?), absent (1?)—*.
7. Moderately or strongly hooked teeth in posterior dentary absent (0), present (1)—1.
8. Procurrent ventral rays 5–10 (0), 9–15 (1)—1.
9. Supramaxillary present (0), absent (1)—1, *.
10. PO_4 level (0), raised (1)—2.
11. Pubic plate narrow (0), wide (1)—1.
12. PO_3 and PO_5 level (0), raised (1)—2.
13. VO_3 level (0), raised (1)—2.
14. PVO horizontal (0), angled (1), vertical (2)—2.
15. Caudal luminous organs present (0), absent (1)—*.
16. AOa_1 level (0), raised (1)–2.
17. Pol angled (0), horizontal (1)—2, *.
18. Enlarged teeth in dentary absent (0), present (1)—1.
19. Vertebrae 28–41 (0), 41–45, (1)—1, *.
20. VO_2 level (0), elevated (1)—2.
21. Enlarged dentigerous area on anterior premaxillary absent (0), present (1)—1.
22. Secondary photophores absent (0), present (1)—1.
23. Larval gut moderate (0), initially short (1), long (2)—3, *.
24. Larval trunk myoseptal pigment absent (0), present (1)—1, 3.
25. Slightly hooked teeth in posterior dentary absent (0), present (1)—1.
26. Caudal luminous organs not sexually dimorphic (0), sexually dimorphic (1)—*.
27. Larval photophores (except Br_2) absent (0), present (1)—1, 3, *.
28. Hyomandibular foramen behind anterior head (0), in anterior head (1)—1.
29. Accessory luminous tissue absent (0), present (1)—1.
30. Caudal luminous organs any other state (0), homogeneous and translucent (1)—*.
31. Procurrent ventral rays without hooks (0), with hooks (1)—1.
32. Procurrent dorsal rays without hooks (0), with hooks (1)—1.
33. Crescent of white tissue on posterior iris absent (0), present (1)—1.
34. Pol 0 (0), 1 (1), 2–3 (2)—2, *.
35. Dorsal process of opercular head of hyomandibula absent (0), present (1)—1.
36. SAOs weakly angled (0), strongly angled (1)—2, *.
37. Larval eyes moderate (0), very large (1)—1, 3.
38. PLO level with PVO_1 (0), above PVO_1 (1)—2.
39. SAO 2, close to VO and AO series (0), 2–3 above VO and AO series (1)—2.
40. Larval pectoral fin moderate (0), large (1)—3, *.
41. Mouth terminal (0), subterminal (1)—1.
42. Antorbital broad (0), thin (1)—1.
43. Larval fin fold small (0), extensive (1)—1, 3.
44. PLO below (0) opposite or proximate to upper pectoral base (1), far above upper pectoral base (2)—2.
45. Lower pharyngeal teeth conical (0), pegs or plates (1)—1.
46. Nasal trough-shaped (0), convex (1)—1.
47. Larval lower pectoral ray not elongate (0), elongate (1)—1, 3.
48. Gill rakers lathe-like (0), as tooth plates (1)—1.
49. Dorsal hypurals 4 (0), 3–2 (1), 1 (2)—1.
50. Coracoid fenestra present (0), absent (1)—1.
51. Double row of isthmus pigment in larvae absent (0), present (1)—1, 3.
52. Premaxillary teeth conical (0), flattened (1)—1.
53. Larval pectoral base fan-shaped (0), wing shaped (1)—1, 3.
54. Larval head pigment present (0), absent (1)—1, 3.

TABLE 63. CONTINUED.

55. Larval choroid tissue absent (0), present (1)—1, 3.
56. Larval body width moderate (0), thin (1)—1, 3.
57. Larval gut uniform (0), bipartite (1)—1, 3.
58. Ossified distal pectoral radials 0 (0), 1–7 (1)—1.
59. CO_5 keel or ridge absent (0), present (1)—1, *.

group (the alepisauroids plus synodontoids) in his arrangement of the order. We do not have further evidence to present in favour of any of the above hypotheses (but do note the coiled gut of neoscopelid larvae resembles the condition found in higher groups).

GENERIC RELATIONSHIPS

Paxton (1972) analyzed features of the osteology and photophore patterns of the Myctophidae and presented a taxonomy outlining his views of evolutionary relationships that included two subfamilies (Myctophinae and Lampanyctinae), six tribes (Myctophini, Gonichthyini, Notolychnini, Lampanyctini, Diaphini and Gymnoscopelini), 28 genera and two subgenera. The Myctophinae was considered the more primitive of the subfamilies, while the monotypic Notolychnini was provisionally placed in the Lampanyctinae. In four papers Moser and Ahlstrom (1970, 1972, 1974; Ahlstrom et al., 1976) detailed the larval characteristics of all but two genera of Myctophidae and translated their findings into a picture of evolutionary relationships. The relationships proposed by Paxton and Moser and Ahlstrom were strikingly similar overall and in many details. The larval studies supported the recognition of two subfamilies composed of the same genera indicated by the adult analysis, highlighted the enigmatic features of *Notolychnus,* and recognized three additional tribes in the Lampanyctinae. Notable differences in the conclusions of the two studies included consideration of the Lampanyctinae as the most primitive subfamily by Moser and Ahlstrom, non-recognition of the tribe Gonichthyini (*Tarletonbeania, Loweina, Gonichthys, Centrobranchus*) as a monophyletic taxon in the larval study, inclusion of the genera *Taaningichthys, Lampadena, Bolinchthys, Lepidophanes* and *Ceratoscopelus* in the tribe Gymnoscopelini by Moser and Ahlstrom and the tribe Lampanyctini by Paxton, and recognition of the genera *Metelectrona* and *Parvilux* as valid genera on the basis of larval characters, which Paxton had synonymized with *Electrona* and *Lampanyctus* respectively on the basis of adult features. Neither study restricted characters to the derived state and the proposed phylogenies were based on overall similarities. The present work will attempt an analysis of derived character states and re-examine the proposed relationships within the family.

We have used as character states (Table 63) features of adult osteology and photophore patterns as described by Paxton (1972), and features of larvae as described by Moser and Ahlstrom (1970, 1972, 1974) and Ahlstrom et al. (1976) summarized in Moser et al. (this volume). The distribution of the character states among the genera (we have not considered subgenera in this analysis) is tabularized (Table 64). The criteria for determining apomorphic character states have been considered by many, including Marx and Rabb (1972) and Zehren (1979:153). We have used three criteria, the numbers of which are listed after each character in Table 63: (1) Outgroup com-

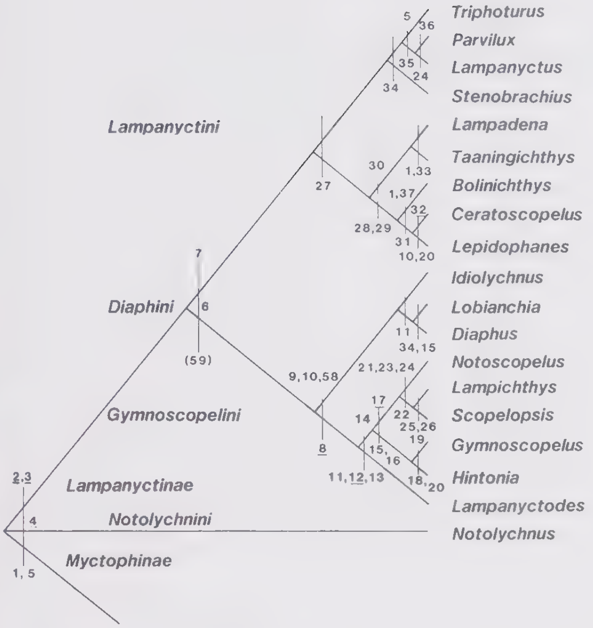
5
36
Triphoturus
Parvilux
35
24
Lampanyctus
34
Stenobrachius
Lampanyctini
Lampadena
30
1,33
Taaningichthys
27
1,37
Bolinichthys
32
Ceratoscopelus
28,29
31
Lepidophanes
10,20
7
Idiolychnus
Diaphini
6
Lobianchia
11
Diaphus
34,15
(59)
9,10,58
21,23,24
Notoscopelus
Lampichthys
17
Gymnoscopelini
14
22
Scopelopsis
25,26
19
8
15,
Gymnoscopelus
16
2,3
11,12,13
18,20
Hintonia
Lampanyctinae
Lampanyctodes
4
Notolychnini
Notolychnus
Myctophinae
1, 5

Fig. 125. Phylogenetic diagram of the Myctophidae, subfamily Lampanyctinae. Numbers refer to the apomorphic characters described in Table 63. Numbers in the middle of vertical lines (e.g., 4, 6) refer to characters for which the apomorphic state is unknown. Underlined numbers refer to apomorphic states unique to all members of a given lineage; bracketed numbers (e.g., 59) refer to apomorphic states that have secondarily reversed in at least one member of the lineage; non-bracketed, non-underlined numbers refer to character states found in all members of a given lineage but also by convergence in at least one other taxon in the family.

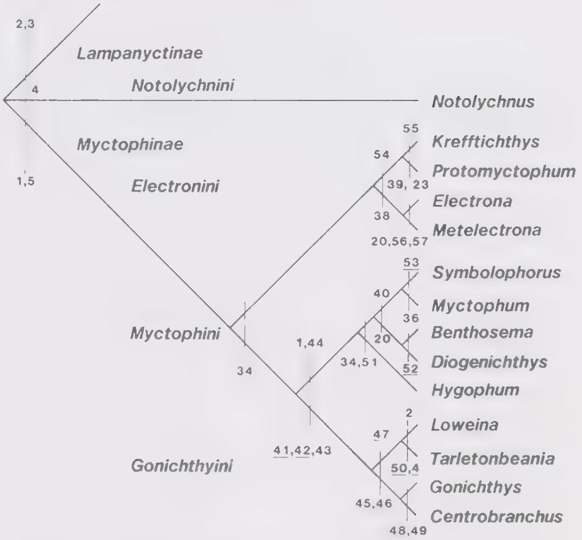
2,3
Lampanyctinae
4
Notolychnini
Notolychnus
55
54
Krefftichthys
Myctophinae
Protomyctophum
1,5
Electronini
39, 23
Electrona
38
Metelectrona
20,56,57
53
Symbolophorus
40
Myctophum
36
Myctophini
Benthosema
1,44
20
34,51
Diogenichthys
34
52
Hygophum
2
Loweina
47
Gonichthyini
41,42,43
Tarletonbeania
50,4
Gonichthys
45,46
Centrobranchus
48,49

Fig. 126. Phylogenetic diagram of the Myctophidae, subfamily Myctophinae. Numbers are defined as in Fig. 125.

parison. All previous workers have considered the Myctophidae and Neoscopelidae as sister groups; we have taken the character state in the Neoscopelidae to be the plesiomorphic condition for the Myctophidae. Paxton (1972:57) described the parallel evolutionary trends in the neoscopelids and myctophids, with *Solivomer* similar to the Lampanyctinae and *Neoscopelus* similar to the Myctophinae. We have largely limited our analysis to those characters which display only one state in the Neoscopelidae. Where variation occurs within the family, the character is discussed individually below. (2) Linear photophores. We have considered a photophore elevated out of linear series to be apomorphic. One line of support for this decision occurs in the ontogeny of those myctophid species with a larval PLO photophore, which develops on the pectoral base (where it presumably has a different function from that of the adult) and moves dorsally during development (Ahlstrom et al., 1976:Fig. 4). Also the photophores of *Neoscopelus*, the only luminous neoscopelid genus, are largely linear. However there is some question of the homology of *Neoscopelus* and myctophid photophores. O'Day (1972:71) described the ultrastructure of myctophid photophores and ". . . confirm(s) Brauer's (1908) original recognition of the close resemblance of photogenic tissue in the Neoscopelidae to that found in the Myctophidae." However Herring and Morin (1978:318) considered photophores of *Neoscopelus* and the myctophids to be very different, on the basis of Kuwabara's (1954) description of *Neoscopelus* compared to that of Brauer (1908). As ventral photophores have evolved independently at least one other time in the stomiiform fishes (Fink and Weitzman 1982:71), the potential for such evolution in deeper water fishes is high enough that one cannot consider their mere existence a case for homology. A study of the ultrastructure of *Neoscopelus* photophores would be of value. (3) Generalized larvae. The larvae of neoscopelids are highly specialized with a robust body, a large head and jaws with prominent teeth, a long gut that may be coiled and large pectoral fins. We do not think these features were present in the ancestors of the two families, and where they are present in the myctophids, consider they have evolved independently. We have used only one such feature, large pectoral fins (40, Table 63) in our analysis. We consider the generalized larva of the myctophid ancestor had the following characters, based on the distribution of larval features in myctophids and other teleosts: body moderately slender, gut slightly S-shaped, extending to about midbody, head moderate in size, eyes round or nearly so, without stalks or choroid tissue, small or moderate finfold and fins and Br_2 the only larval photophores present.

We have used a total of 59 characters, far fewer than the total described in the previous studies. For many we were unable to determine a derived state, as they displayed two or more states or were absent in the neoscopelids. In the osteological descriptions small shape differences or classifications of a continuum were often found in both families and were not included. A number of the characters utilized require comment or explanation: (1) Jaws are long in *Solivomer* and short in *Neoscopelus*, and following our ground rules should not be utilized. However, they appear to be of such fundamental importance, affecting many correlated characters and appearing to represent a major subfamilial difference (Paxton, 1972), that they are included here. Paxton (1972:58) considered short jaws to be primitive, primarily because they occurred in *Protomyctophum*, thought

TABLE 64. CHARACTER STATES IN THE GENERA OF MYCTOPHIDAE. The 59 characters are described in Table 1. 0 = plesiomorphic state, 1 – apomorphic state, 2 = different or advanced apomorphic state, 9 = unknown or both states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Krefftichthys	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Protomyctophum	2	0	0	1	1	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Electrona	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
Metelectrona	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
Benthosema	2	0	0	1	1	9	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	9	0	0	1	1
Diogenichthys	2	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Hygophum	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Myctophum	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	9	0	0	1	9
Symbolophorus	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	1	0
Loweina	1	2	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	1	0
Tarletonbeania	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0
Gonichthys	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Centrobranchus	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Notolychnus	0	9	0	1	9	0	0	0	1	9	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0
Lobianchia	0	1	1	0	9	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1
Diaphus	9	1	1	0	0	0	0	0	1	1	1	0	1	1	1	9	0	9	0	1	0	0	0	0	0	0	1
Idiolychnus	0	1	1	0	9	0	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	9	9	0	1	9
Lampanyctodes	0	1	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Gymnoscopelus	0	1	1	0	0	0	0	1	0	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	1
Scopelopsis	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	9	0	1	0	0	1	1	1
Lampichthys	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	1
Notoscopelus	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	1
Hintonia	0	1	1	0	9	0	0	1	9	0	0	0	0	2	1	0	9	1	0	1	0	1	9	9	1	0	9
Lampadena	0	1	1	0	0	1	1	0	1	9	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	1
Taaningichthys	1	1	1	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
Ceratoscopelus	1	1	1	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
Lepidophanes	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	1
Bolinichthys	2	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	1	9	0	0	0	0	1
Triphoturus	0	1	1	0	1	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0
Stenobrachius	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0
Parvilux	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Lampanyctus	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	9	0	9	0	1	0	0	0
Solivomer	0	1	0	9	9	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	9	9	0	0	9
Neoscopelus	2	1	0	9	0	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	0	0	0	0	0
Scopelengys	0	1	0	9	0	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	0	0	0	0	0

to represent the most primitive myctophid based on photophore pattern. However Myers (1958) has shown that short jaws have arisen from the long-jawed condition a number of times in teleost evolution, and discussed their adaptive advantages. We consider short jaws to be the apomorphic condition within both the Myctophidae and Neoscopelidae, and moderate jaws also to be derived from long jaws. (2) Extrascapulars are single in neoscopelids; therefore two extrascapulars in some myctophids should be the derived condition. However Paxton (1972:58) described how the neoscopelid extrascapular differs in position and shape from that of myctophids. Following Williston's Rule we consider a single extrascapular to be derived from the fusion of two elements, independently attained in each family. In *Loweina* the single condition has arisen through the loss of the dorsal extrascapular. (4) With no outgroup with similar photophores for comparison, we are unable to determine whether 1–2 or 3–9 Prcs is the apomorphic state. However the two character states follow subfamilial limits, and one of the states must be derived and definitive for its subfamily. (6) All myctophids have at least one of the orbital light organs, Dn and Vn, and most have both. We are not sure whether the presence or the absence of a Dn is apomorphic, but one of those states defines a major line within the Lampanyctinae. (9) Although the Neoscopelidae have a supramaxillary, Paxton (1972:62) considered the supramaxillary of some Myctophidae to be an independently derived feature, due to a difference in shape and its required loss at least four times within the family if considered primitive. However, Johnson (1974b:205, 1982:79) has shown the presence of supramaxilla(e) to be primitive in other myctophiforms (*sensu lato*); the absence of a supramaxilla in myctophids is here considered a derived state through loss. (15) Although caudal luminous organs are not present in neoscopelids, they are present in all but three myctophid genera, where their loss is here considered derived. No other characters indicate that any of the three genera (*Diaphus, Gymnoscopelus, Hintonia*) are the most primitive in the family. (17) Two or three horizontal Pols are in a linear position and should be considered the plesiomorphic condition. However in those genera with horizontal Pols (*Notoscopelus, Lampichthys* and *Scopelopsis*) the photophores are high, close to the lateral line. We consider the primitive myctophid state to be one with low photophores with none or one Pol (character 34). We therefore consider the horizontal position of Pols to be derived, while noting the state in *Hintonia* is intermediate between angled and horizontal. (19) Although Johnson (1982:76) considered a higher number of vertebrae (42–62) plesiomorphic for iniomous fishes, lower numbers of vertebrae in neoscopelids and almost all myctophids indicate the higher number in *Gymnoscopelus* is a secondary specialization in these families. (23) The larval gut of some neoscopelids is long and coiled, clearly a specialization foreshadowing the condition of

TABLE 64. EXTENDED.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	0
1	0	0	0	0	0	0	0	9	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	9	0
1	0	0	0	0	0	9	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0
1	0	0	0	0	0	1	0	9	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	9	0	0	1	0
1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0
1	0	0	0	0	0	2	0	9	0	1	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	9	9	9	1	0
1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	9	2	9	0	0	0	9	0	0	0	0	0	1	0	0	9	0
1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	1	0	0	9	0
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	2	0	0	0	0	0	1	1	0	1	0
0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	9
1	0	0	0	0	0	9	0	0	0	1	1	1	0	0	0	2	0	0	0	0	9	0	0	0	0	1	9	0	0	1	1
9	9	0	0	0	0	9	0	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	1	0	0	0	1	9
1	0	0	0	0	0	2	0	0	9	1	1	9	0	0	9	2	0	0	9	0	9	0	9	0	9	9	9	9	9	1	9
0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
9	1	0	0	0	0	2	9	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	1
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	1	0	0	0	0	2	0	0	9	1	1	9	0	0	9	2	0	0	9	0	0	0	9	0	9	9	9	9	9	0	0
0	9	1	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	1	1	0	2	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	0	1	0	0	2	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
1	1	0	0	0	1	2	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	2	0	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	1	9	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	2	1	0	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	9	0	0	0	0	2	1	1	9	1	1	9	0	0	0	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	9	0	9	9	9	9	9	0	0	9	9	0	0	9	0	0	0	9	0	9	9	9	9	9	0	0
0	0	0	0	0	0	9	0	9	0	9	9	1	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	9	0	9	0	9	9	1	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

some acanthopterygians. Although it could be argued that the short gut that lengthens during development in a few forms of myctophids represents the primitive condition, we consider the primitive myctophid condition a moderate—lengthed gut, with different derived states, short and long. (26) Although the caudal luminous organs are sexually dimorphic in about half the genera, we assume the original caudal organs were not sexually dimorphic. (27) No photophores are present on the described larvae of *Neoscopelus.* However the Br_2 develops in all larval myctophids except *Taaningichthys* and *Notolychnus,* and its universality indicates it was present in the ancestral myctophid. Other larval photophores however are present in fewer than half of the genera and we consider their presence derived. (30) The strongly developed caudal luminous organs found in *Lampadena* and *Taaningichthys* are clearly a more specialized state than the relatively unstructured organs found in many other genera. (34) See the discussion of character 17. (36) Although a strongly angled set of SAOs represents a linear position for the first two photophores, we consider this condition developed by the SAO_1 rising from a lower position in the weakly angled, plesiomorphic position. (59) We consider the absence of a keel or ridge on the fifth circumorbital of *Hintonia* to be secondarily derived through loss. This is the only character state we have used which is not present in all examined members of the line it defines.

We have thus attempted to determine polarity for 25 osteological, 17 larval and 17 photophore characters. We initially attempted a phylogenetic analysis utilizing the distribution of 23 larval characters at the species level. The resulting diagram split some genera into as many as three unrelated lines. We remain convinced that the myctophid genera as currently defined by larval morph, photophore pattern and osteology represent monophyletic lines (even though such genera as *Diaphus, Lampanyctus, Myctophum* and *Hygophum* may be formally divided as subgenera or genera by future work). These genera we use as the starting point in the present study. We have constructed a phylogenetic tree (Figs. 125, 126) based on our knowledge of the family and used the apomorphic states of the 59 characters to define the various branching points, which is the basis of the following discussion.

The subfamily Lampanyctinae is defined by two apomorphies restricted to all members of the subfamily (those characters found in all members of a lineage and nowhere else in the family are underlined in Figs. 125 and 126), the presence of a cleithral shelf and a single, fused extrascapular. The subfamily Myctophinae is defined by two apomorphies, short or moderate jaws and narrow larval eyes, but these features are also found in a few genera of the Lampanyctinae. The number of Prc photophores defines all members of one of the subfamilies (see discussion of character 4 above).

Notolychnus valdiviae, here considered a monotypic tribe, could not be placed with certainty in either subfamily. Moser and Ahlstrom (1970:138, 1974:409) and Paxton (1972:61) discussed the characters and problems of this enigmatic species. With long jaws and the lack of a cleithral shelf both considered plesiomorphies, the apomorphic number of Prc photophores unknown, and the larval eyes variable and intermediate in shape, future work is required to resolve this trichotomy.

We recognize three tribes in the subfamily Lampanyctinae (Fig. 125). The tribe Lampanyctini, with nine genera, is defined by the presence of a row of moderately to strongly hooked teeth in the posterior dentary; the only other genus with this feature is the myctophine *Diogenichthys.* These nine genera are also the only lampanyctines to lack a Dn orbital photophore, but we are unsure if this is a derived state (see discussion of character 6 above). Moser and Ahlstrom (1972) and Ahlstrom et al. (1976: 148) placed five of these genera (*Lampadena, Taaningichthys, Bolinichthys, Lepidophanes, Ceratoscopelus*) in the tribe Gymnoscopelini, based primarily on larval photophore pattern. Photophores which appear in larvae of Lampanyctinae are essentially the same ones which develop in myctophine larvae (Moser et al., this volume) and, if they are adaptive as Moser (1981) has suggested, it is likely that they have appeared in these typical sites independently in a number of lineages. Moreover, these photophores develop at the end of the larval period, if at all, in *Bolinichthys* and no photophores develop in *Taaningichthys* larvae. Likewise, the larval pigment characters do not support the inclusion of these five genera in the Gymnoscopelini.

In addition to the distribution of hooked dentary teeth and Dn photophores, other features influenced our decision about these five genera. The ischial ligament is medium or long in all Lampanyctini except *Taaningichthys* (and some species of *Diaphus*), while the fifth circumorbital has a ridge or keel in all gymnoscopelines (but is lacking in some species of *Diaphus*) and no lampanyctines except *Bolinichthys* (thus the brackets around character 59 in Fig. 125). Finally all of the gymnoscopeline genera except *Notoscopelus* are restricted to the southern ocean (Moser et al., this volume: Table 59), while the Lampanyctini are found both north and south (except *Stenobrachius*) of the equator. Placement of the five genera in the Lampanyctini requires fewer character reversals and parallelisms.

Within the Lampanyctini, the development of larval photophores in addition to Br_2 (character 27) unites the five genera discussed above. We recognize *Dorsadena* as a subgenus of *Lampadena* until specimens other than the types are available for osteological study and the larvae are discovered. We have not found an apomorphic character that defines the line including *Stenobrachius, Triphoturus, Lampanyctus* and *Parvilux.* We are recognizing *Parvilux* on the basis of a weakly angled SAO and larval shape and pigmentation.

We consider the tribe Diaphini to be the sister group of the Gymnoscopelini. The relationships among the three genera of Diaphini are not clear. One of us (HGM) has re-examined the specimens on which the larval features of *Idiolychnus urolampus* were based (see Moser and Ahlstrom, 1974:405–406; Nafpaktitis and Paxton, 1978), and now thinks they could represent *Lobianchia gemellari,* with the larvae of *Idiolychnus* still unknown. Two characters shared by *Lobianchia* and *Idiolychnus,* the presence of caudal organs and the absence of a luminous patch above the pectoral fin, are considered plesiomorphic, while the absence of a Vn and differences of photophore positions are not clearly apomorphic. The most unequivocal derived state is the presence of a wide pubic plate, indicating *Lobianchia* and *Diaphus* are the sister group pair.

Within the Gymnoscopelini the proposed generic relationships are based almost entirely on characters of the photophores and luminous tissue. No consistent osteological or larval features define generic groupings. Southern ocean larvae require more study. The larvae of *Hintonia* are unknown and not enough species of *Gymnoscopelus* have been studied to ascertain if the subgenus *Nasolychnus* can be defined by any larval characters. The species of *Notoscopelus* should also be studied to find supporting characters of the subgenus *Parieophus.*

Within the subfamily Myctophinae (Fig. 126), we also recognize three tribes, the Electronini, Myctophini and Gonichthyini. The Gonichthyini is clearly a derived lineage, with a number of osteological, photophore and larval characters distinguishing the four genera from the rest of the subfamily. We think the larval specializations of eyes and pectoral fins arose after the split of the two generic pairs.

Paxton (1972) was unable to find osteological characters to clearly separate the remaining genera of the Myctophinae into two lineages. We have utilized photophores to distinguish the Myctophini from the Electronini, while recognizing there is a mosaic of osteological and larval characters within these nine genera. We have little question of the sister group relationship of the generic pairs *Krefftichthys—Protomyctophum, Myctophum—Symbolophorus* and *Benthosema—Diogenichthys.* However two larval features, thin head and body and a bipartite gut, are shared by *Metelectrona* and some species of *Hygophum.* Since we think *Hygophum* is a monophyletic line, we consider these shared larval features parallelisms that do not indicate common ancestry. Paxton (1972) considered *Metelectrona* a synonym of *Electrona.* The description of a second species of *Metelectrona* (Hulley, 1981), coupled with its larval and photophore characters, convinced us to recognize the genus.

Of the 59 derived characters utilized in our analysis, only 20 are restricted to members of the lineage they define, and eight of these are autapomorphic at the generic level. The remaining 39 characters are not found in the apomorphic state in any member of the opposite lineage from the defined branching point, but are found in some members of other lineages within the family. This presumed homoplasy of larval, photophore and even osteological characters indicates that the proposed phylogeny was arrived at with some difficulty. Ten of our proposed lineages are undefined by derived characters. We think that future work will support our proposed phylogeny, although some details may be modified, and that new, less plastic characters and better definitions of polarity will help resolve the problems.

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Investigation of the Cetacean Fauna and Former Dolphin Fishery of St. Helena

Grant Recipient: William F. Perrin, Southwest Fisheries Center, National Oceanic and Atmospheric Administration, La Jolla, California.[1]

Grant 2543: To determine the identity of dolphins taken in a former fishery and to investigate historic methods, landings, and present status of the fishery.

The cetacean fauna of St. Helena has been very poorly known scientifically. Melliss (1875) described "five kinds of cetaceous animals commonly known[:] . . . *B. mysticetus* (right whale?) . . . , *P. macrocephalus* (sperm whale) . . . , Delphinus, Linn. . . . one kind only of Dolphin . . . , Phocaena, Linn. . . . two kinds of porpoise . . . Right Whale Porpoise and the Sperm Whale Porpoise . . . ." No further accounts of the cetaceans inhabiting the waters around St. Helena have been published.

Determining the identity of dolphins taken in a small harpoon fishery at St. Helena is important to an ongoing taxonomic study of the dolphins of the genus *Stenella* of the Atlantic. Spotted dolphins in the Atlantic have been referred to in recent years as *Stenella frontalis, S. attenuata, S. plagiodon, S. capensis,* and *S. dubia.* The holotype specimens of all these nominal species consist of skulls only. Unfortunately, our emerging picture of the two apparently valid species shows them to differ markedly not in skull characteristics but in color pattern and vertebral count, data not available for the holotype specimens. To solve this problem we plan to gather skull measurements from all available specimens that are referable to one or the other of the two species based on color patterns or vertebral count, to construct discriminant functions (an analytical technique involving simultaneous consideration of a large number of variables), and finally to apply the discriminant function to the holotype specimens, so that they (and the names they carry) can be assigned to one or the other of the species.

For one of the species, an endemic form to which the name *S. plagiodon* has been most commonly applied, there are a large number of fully documented specimens in museums in the United States. Atlantic specimens of the second species, a pantropical form most recently called *S. attenuata* or *S. frontalis,* are much less abundant. We have located only 16 with data on coloration or vertebral count. However, the British Museum has 41 skulls of spotted dolphins taken from St. Helena by local fishermen, mostly in the late 1950s. The skulls came without information on coloration or skeleton but exhibit very low variation, indicating they are all of a single species. The one (ventral) photograph of a St. Helena dolphin in the British Museum Archives shows a color pattern more consistent with that of the pantropical species than with the Atlantic endemic species, but the angle of the photograph prohibits a firm conclusion. We hoped color pattern would identify the type of dolphin taken by the fishermen in St. Helena. If it proved to be the pantropical species, then the large series of skulls in the British Museum could be used in the discriminant analyses aimed at resolving the taxonomic problem.

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[1] Marilyn J. Perrin assisted the grant recipient on this project.

Research

We observed and photographed dolphins on the lee side of the island from an open fishing boat on five days between May 5 and June 2, 1983. Our usual observation strategy was to make multiple passes through a moving school, taking photographs on the down-swell legs. On May 5 and 26, we observed and photographed the animals underwater.

On May 25, we sailed around the island to observe cetaceans on the south side. However, the weather was very rough, and we saw no cetaceans.

We tape-recorded interviews with 10 fishermen and 1 boat owner concerning the history, methods, catches, and economics of the dolphin fishery, and had more informal discussions with an additional 35 to 40 individuals, including government officials and employees of the St. Helena Fisheries Corporation. We asked for information on the dolphin fishery through a notice in the island newspaper and on a local radio broadcast. We spent several days scanning and abstracting information from books, official records, and 19th-century newspaper files maintained in the island library and archives. Because of lack of time, we examined only a fraction of the material in the archives.

Cetacean Fauna

Pantropical Spotted Dolphin, *Stenella* sp.

This was the dolphin most commonly harpooned in the fishery. Island fishermen call it "bottlenose porpoise" or simply "porpoise." The skulls in the British Museum are of this species. We clearly observed diagnostic color-pattern characteristics: white-tipped beak, well-defined cape passing high over the eye and with greatest depth at the level of the dorsal fin, narrow light band subsidiary to the cape, flipper stripe to gape, and dorsoventral division of the peduncle into upper dark and lower light areas. Calves are unspotted, and juveniles have pronounced dark spots below. Dorsal spotting in adults is so poorly developed as to appear absent when the animals are seen at a distance of a few meters.

The school that we observed consisted of several hundred dolphins. It came into shallow water within 0.5 km of shore along the southern half of the lee side of the island in the early morning and moved slowly north and headed back offshore at the northern lee edge before noon. During this slow passage the school appeared to be loosely organized and dispersed over a distance of about 0.5 km in subgroups of about 5 to 10 animals. Groups milled, briefly reversed direction, and made short forays offshore. Aerial activity, including high leaps (mostly by juveniles), forward flips, pitch-poling, and tail lobbing, was extensive. Occasional intense flurries of surface activity involving two or more animals was evidenced by violent, confused splashing.

On each occasion as we approached the school, individual dolphins came to meet the boat and rode the bow briefly. They did not surface at the bow to breathe, but moved a few meters away from the boat, blew, and returned to the bow underwater. This differs from typical bow-riding behavior, in which the animals surface to breathe at the bow, and may be related to the fishermen's practice of harpooning dolphins from the bow.

On one day we followed the dolphins to the edge of the lee, where part of the school spent several minutes "surfing" in short steep swells. Some of the dolphins made several passes in the waves, doubling back after traveling 100 m or so.

Fishermen told us that once the school goes offshore, out of the lee of the island, it breaks into several smaller schools. These may be encountered several kilometers offshore in the afternoon. They are occasionally seen on the weather side of the island. Fishermen also said that dolphins are "easiest to find" in April and May.

BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*

This dolphin is called "cowfish" or "cow porpoise," but some fishermen also call it "angerine." It was taken in the fishery in lesser numbers than the spotted dolphin. Several skulls of this species are in the British Museum.

We observed this dolphin at least twice. On May 5, we saw several large dark dolphins with high falcate dorsal fins in the school of spotted dolphins. The fishermen called these cowfish; but we did not get a good look at them. On June 2, we encountered and photographed a small school (10 to 15) of bottlenose dolphins at 0830 hours. As we approached, the animals evaded us by diving for several minutes and coming up about 200 m away. We identified them by their size, coloration, size and shape of dorsal fin, and shape of the head (a short beak sharply demarcated from the melon). On June 5 at 1420 hours, as we left the island, several bottlenose dolphins joined the ship 5 to 7 km offshore and rode the bow and stern wakes for about 10 minutes.

Fishermen told us that cowfish sometimes frequent James Bay at night, feeding on flying fish attracted to lights on the waterfront.

An officer on the R.M.S. *Centaur* showed us a videotape of several bottlenose dolphins riding the bow of the ship just off Ascension Island, about 700 nm northwest of St. Helena, on March 12, 1983.

Other Species

Only two species other than spotted and bottlenose dolphins can be said with certitude to occur (or have occurred) at or near St. Helena: the humpback whale and the spinner dolphin, *Stenella longirostris.* Inclusion of the spinner dolphin is based on a skull in the Cleveland Museum of Natural History (No. 2413) labeled as collected at St. Helena by the Blossom South Atlantic Expedition on October 10, 1926. Fishermen to whom we talked did not recognize photographs of spinner dolphins nor did they remember having seen its distinctive spinning behavior. The inclusion of the humpback in the fauna is based on 19th-century newspaper and whaling accounts.

Fishermen told us of a seasonal occurrence or past strandings of several kinds of large whales which they called "humpback," "sperm," "blue," or "right whales," but these reports are not confirmed by specimens or photographs. They also reported occasional or seasonal occurrence of "whale killers," "blackfish," "whitebelly porpoise," and "black porpoise" with blunt heads.

While some of the fishermen use angerine (or "angeline") when referring to the bottlenose dolphin, most use this term to refer to a quite different animal. Our most reliable and conservative informant, a retired fisherman, described the angerine as a little larger than a cow porpoise (which he has measured up to 8 ft long), dark above and cream-colored below, with a few (four to five) white spots on each side and a short beak. He said the animal occurs in groups of a dozen or so, never in the company of other dolphins. Others described the angerine as larger than the cowfish and with a few spots (pink or white and about an inch in diameter) and a white or pinkish belly. Murphy (1947) reported that whalemen used the term "algerine" (possibly derived from "Algerian") for small beaked whales of the genus *Mesoplodon,* but it is very unlikely that this is the usage at St. Helena. The descriptions are most consistent with characteristics of the rough-toothed dolphin, *Steno bredanensis;* however, this is a highly tentative conclusion. The angerine was only rarely harpooned by the islanders and is said to fight harder than other porpoise.

The inclusion by Melliss of the right whale dolphin *(Lissodelphis peronii)* in the fauna of St. Helena seems questionable, as it is a cool-temperate species and the waters around St. Helena are tropical, albeit seasonally verging on warm-temperate.

DOLPHIN FISHERY

A fuller account of the dolphin fishery will be submitted to the Scientific Committee of the International Whaling Commission.

The dolphin fishery likely had its origins in 19th-century whaling; the whalemen harpooned dolphins for practice and for consumption by the crew. This thesis is supported by the islanders' use of Yankee whaling terms such as porpoise, cowfish, algerine, blackfish, and "iron" (for harpoon), and by the implements used in the fishery, which until the 1960s were modeled on sperm-whaling gear.

The pursuit of dolphins has always been an adjunct to other fishing activities. Typically, a dolphin or two was harpooned on the way home from the tuna-fishing grounds after a day of low tuna catch. Before World War II, sails were used. In the 1950s and 1960s the boats converted to small diesel engines, which made catching dolphins easier. A very few bottlenose dolphins were harpooned in the harbor at night. Average annual catches before 1979, when the taking of dolphins was banned, were on the order of 100 to 200 spotted dolphins and 5 to 15 bottlenose dolphins a year, perhaps peaking in the 1950s. Records of landed dolphins sold to the Fisheries Corporation were only kept for 1978, when 37 dolphins were logged (some landed dolphins were not sold to the Corporation). As recalled by the fishermen, the usual daily take by a boat was one or two dolphins. Dolphin meat was highly esteemed, and, when available, brought about the same price as tuna. Despite the ban, a few dolphins (perhaps 5 to 10 annually) are still taken for consumption by boat crews or family use; but dolphin meat no longer appears in the market.

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Patterns of geographical variation in small cetaceans

W.F. Perrin

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Morphological data that have become available in recent years show that small cetaceans vary sharply over sometimes relatively short distances. Species for which such data are reviewed include *Stenella attenuata, S. longirostris, Delphinus delphis*, and *Tursiops truncatus*. Two major patterns are variation between animals in enclosed vs. open seas and in offshore vs. inshore waters. An hypothesis of ecological character displacement is proposed to account for differentiation of races of *S. longirostris* in the central and eastern Pacific. Prevalence of pronounced geographical variation must reflect relatively high localization of populations and suggests that great care should be taken in the exploitation of small cetaceans to insure that the population unit has been adequately defined. Harvest quotas taken in limited areas but based on supposed existence of larger-scale populations could lead to local depletion if the population units are more circumscribed than thought.

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1. Introduction

Man exploits small cetaceans heavily. The estimated annual take exceeds 100 000 dolphins, porpoises and small whales (Perrin 1982). In recent years, considerable effort has been given to managing the impacted populations of small cetaceans on a scientific basis (Fox 1978, Scientific Committee, IWC 1976—1981). A major first step in this management is to define the populations involved. One tool for defining mammal populations is the analysis of geographical variation in morphology. Close study of adequate material, as in the case of the eastern Pacific (Perrin 1975a, 1975b, Perrin et al. 1979) and elsewhere, has revealed existence of sharply defined variation over relatively small distances in pelagic dolphins, and this has been reflected in scientific advice for management (Smith 1979). The purpose of this paper is to review apparent patterns in geographical variation and to briefly discuss implications for management and for taxonomy.

2. Patterns of variation

2.1. Enclosed seas vs. the open ocean

Dolphins in enclosed or semi-enclosed seas tend to be smaller than those of the same species in the open ocean. The most noted example of this "dwarfism" is in populations of the common dolphin, *Delphinus delphis*, and bottlenose dolphin, *Tursiops truncatus*, in the Black Sea, as described by Kleinenberg (1956). Common dolphins in the Black Sea are on the average 30—40 cm smaller than common dolphins in the eastern North Atlantic (Table 1). Although the samples are small, it appears that common dolphins in the Mediterranean, a larger but also enclosed sea, may be intermediate in size between those in the Black Sea and in the eastern North Atlantic.

Maximum-length data for the bottlenose dolphin from the three regions indicate that it follows the same pattern as the common dolphin, i.e., small animals in the Black Sea, large animals in the eastern North Atlantic, and animals of intermediate size in the Mediterranean (Table 2).

2.2. Inshore vs. offshore

This is the largest category of known cases of geographical variation. I will discuss examples of this type of variation in dolphins of the genera *Stenella, Delphinus* and *Tursiops*.

The pantropical spotted dolphin, *Stenella attenuata*, and the spinner dolphin, *S. longirostris*, each occur in several geographical races in the eastern and central tropical Pacific (Perrin 1975a, 1975b, Perrin et al. 1979, Smith 1979). There are two major forms of *S. attenuata* in the eastern Pacific, a relatively large, heavily spotted coastal form with massive jaw musculature and large teeth and a relatively small, less spotted offshore form with more lightly constructed skull and jaw musculature and smaller teeth. These two forms have been called *S. graffmani* (Lonnberg 1934) and *S. attenuata* (Gray 1846), respectively, in the past, but studies of large series of specimens have shown them to intergrade (Perrin 1975a).

Moving north in the eastern Pacific to temporate waters the common dolphin, *Delphinus delphis*, and bottlenose dolphin, *Tursiops truncatus*, exhibit inshore/offshore variation similar to that of the tropical *Stenella* spp. Banks & Brownell (1969) reviewed *Delphinus* in the eastern North Pacific. They referred a short-beaked form to *D. delphis* and a long-beaked form to *D. bairdii*. Evans (1975), however, found intergradation between the two forms and assigned them both to *D. delphis*. In subsequent assessment and management advice, these have been called the "Baja neritic common dolphin" and the "northern temperate common dolphin"

Table 1. Body-length data, in cm, for common dolphins, *Delphinus delphis*, from three different regions. (Sources summarized in W.F. Perrin & S.B. Reilly, MS). Sample sizes in parentheses.

	Average length of adults		Maximum length	
	Males	Females	Males	Females
Eastern North Atlantic	218 cm (17)	203 (26)	258 (168)	230 (169)
Black Sea	—	171 (198)	219 (> 20000)	200 (> 20000)
Mediterranean	—	—	222 (35)	222 (35)

Table 2. Maximum body length of bottlenose dolphins, *Tursiops truncatus*, from three different regions. Sample sizes in parentheses (Sources summarized in W.F. Perrin & S.B. Reilly, MS).

Region	Males	Females
Eastern N. Atlantic	381 (67)	350 (47)
Black Sea	310 (> 500)	< 310 (> 500)
Mediterranean	330 (14)	320 (6)

(Smith 1979). The inshore Baja neritic form differs from the more offshore northern temperate form in several features. As well as having a proportionately longer rostrum, it is longer overall, ranging in males to over 240 cm and in females to over 220 cm (Hui 1977) as opposed to 200 cm and 190 cm (Evans 1975). The two forms also differ modally in coloration; the overall pattern is much less sharply defined, and the thoracic patch (terminology of Mitchell 1970) is noticeably less yellowish in the inshore form. In addition, the anterior end of the flipper stripe (terminology of Perrin 1969) abuts on the gape mark considerably more posteriorly than in the offshore form. The skull also differs in size and shape in the two forms (Evans 1975).

Similar inshore/offshore variation may exist in *Delphinus* elsewhere. The extremely long-beaked common dolphins that occur in the Indian Ocean and in the South China Sea and which have been referred to the nominal species *D. tropicalis* (van Bree 1971, Zhou et al. 1980) may be inshore animals; the body lengths reported (to 229 cm, Blanford 1881) lie above the ranges of lengths reported for other, larger samples of common dolphins from similar latitudes in the western Indo-Pacific (Tomilin 1957, Ogawa 1936).

Inshore and offshore populations of *Tursiops* in the eastern North Pacific also differ modally, in skull size and shape, tooth size, and possibly in adult body length (Walker 1981). The inshore form has the larger teeth, as in *S. attenuata*. These bottlenose dolphins have been referred to varying permutations of *T. truncatus, T. gilli* and *T. nuuanu*. Most workers today favor a single species, *T. truncatus*. Another example of inshore/offshore variation in *Tursiops* exists along the southeast coast of South Africa; in this case the inshore from (referred to *T. aduncus*) is the smaller and the offshore form (referred to *T. truncatus*) is the larger (Ross 1979). A similar situation may exist along the western North Atlantic, although the large offshore animal has not yet been well studied because of the scarcity of material (pers. comm. James G. Mead, U.S. National Mus. Nat. Hist., Washington, D.C.).

The morphological difference between inshore and offshore races of the various dolphins, especially in the number and size of teeth and in the robustness of jaw musculature, may be related to feeding ecology, perhaps to differing size and toughness of major prey species (Perrin 1975a, Ross 1979).

2.3. Other patterns

Modal differences in body shape and coloration between spinner dolphins, *Stenella longirostris*, in the far eastern Pacific and those in the Central Pacific and around the world in tropical waters are extreme (Perrin 1972, 1975a, 1975b). The spinner dolphins in the far eastern Pacific (the "Costa Rican" and "eastern" forms; see Smith 1979 for ranges) are unique in being nearly uniformly dark gray (as opposed to having a three-part dark-gray, light-gray and white pattern as do spinner dolphins to the west and in other parts of the world) and, in large males, in having the dorsal fin canted forward to varying degree (with correlated development of a ventral post anal "hump" of connective tissue). Spinner dolphins from the regions between the Central Pacific and the far eastern Pacific are intermediate, strong grounds for including all the forms in the single species *S. longirostris*, but the interesting question remains of why the spinners in the far eastern Pacific are so different. I put forward here an hypothesis of *ecological character displacement*. The relevant information concerns morphology, ecology, behavior (Table 2) and oceanography. The hypothesis is suggested by two facts: 1) while both spinner and spotted dophins outside the eastern tropical Pacific are limited in distribution to waters near continents and islands, where they school separately and feed on similar prey, the spinner dolphin is unusual in that it migrates diurnally between offshore feeding grounds and relatively protected bays, where it spends most of day in a quiescent resting state, presumably relying on the shallow bottom and the shoreline for protection from predators (Norris & Dohl 1980), and 2) the far-eastern Pacific is peculiar in having a relatively thin warm mixed layer (50 m thick) below which are a stable steep thermocline and a thick oxygen-minimum layer, establishing an effective shallow habitat much like the nearshore habitat in other tropical waters (Perrin et al. 1976).

The hypothetical scenario of ecological character displacement is as follows: habitat in most of the world for the spinner dolphin is defined by availability of shoreline near suitable food supplies (within range of diurnal migration and not too deep), but habitat for the spotted dolphin is determined only by availability of food within efficient diving range (near continents and islands). In the far-eastern Pacific, because of its peculiar vertical structure that creates a shallow mixed-layer habitat with sharply-defined floor, both animals can "make a living" far from land on the high seas. The spinner dolphins, however, must have a surrogate "shoreline" for shelter during their daytime quiescent period. They use schools of spotted dolphins for this, staying with them even when not feeding (first suggested by Norris & Dohl 1980). In the course of the move into the far-offshore habitat and evolution of the mixed-species association, direct competition for prey by the two species has been minimized by specializations in feeding habits that are reflected in morphological divergence in morphology, the spinner dolphin becoming more adapted to smaller, deep-living prey (hence the more

Table 3. Comparison of morphology (Perrin 1972, 1975a, 1975b), ecology and behavior (Perrin et al. 1973) of *Stenella longirostris* and *S. attenuata* in the Central Pacific with those in the far-eastern Pacific.

	Central Pacific	Far-eastern Pacific
Morphology		
Coloration	Similar (countershaded)	Different (unifrom vs. countershaded)
Body size	Similar (~ 200 cm)	Different (~ 170 vs. ~ 200 cm)
Body shape	Similar	Different (dorsal-fin cant & ventral hump)
Skull size	Similar	Different
Temporal fossa	Similar size & shape	Different
Ecology & behavior		
Feeding habits	Similar (mostly mesopelagic spp.), but few data	Different (mostly smaller, mesopelagic spp. vs. larger, epipelagic spp).
Schooling	School separately	School together
Diurnal migration	Different (inshore migration vs. none)	Same (none)

lightly built feeding apparatus and the loss of counter shading) and the spotted dolphin becoming more adapted to larger, surface-living prey.

Other hypotheses to explain the morphological variation are possible, but this exercise does demonstrate the complexity of factors possibly affecting population structure and points up the importance of considering the full range of oceanographic information (beyond merely single variables, e.g., surface temperature) when attempting to define the habitats and ranges of breeding populations.

3. Conclusions

The findings on geographical variation have had an effect on the taxonomy of the small cetaceans. We have relegated many species to junior synonymy in recent years. This is continuing. For example, Ross (1979) has recently found intergradation between the currently recognized species of humpbacked dolphins, *Sousa chinensis* and *S. teuszii*, in South Africa. As more material accumulates, we may find similar intergradation between nominal species of *Delphinus, Tursiops, Lagenorhynchus, Cephalorhynchus, Mesoplodon* and perhaps other genera.

It would seem that pronounced geographical variation (and the inferred reproductive isolation) is found to exist in small cetaceans in each instance of study of adequate samples of specimens. The import of this for exploitation and management of small detaceans is clear. It cannot be assumed that animals inhabiting adjacent seas, oceans, or even parts of oceans belong to a single population. Definition of management units should be based on knowledge of geographical variation in morphology and autecology and, beyond that, should take into consideration the likely populational divisions predicted by our knowledge of patterns of geographical variation and by knowledge of definable marine habitats and systems.

In summary, then, in the future there will likely be fewer recognized species of small cetaceans, but there will be many more recognized breeding populations that may require assessment and management as separate units.

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Annex H

Report of the Sub-Committee on Small Cetaceans

1. PARTICIPANTS, AGENDA AND INTRODUCTORY REMARKS

Members (M) of the Scientific Committee, invited experts (E), observers (O), and interpreters (I) attending the meeting were:

Aguilar (M), Balcomb (E), Best (E), Braham (M), Broadhead (M), Brown (M), Brownell (M), Cawthorn (E), Collet (E), Christensen (M), Davis (E), Gaskin (E), Glover (O), Gong (M), P. Hammond (O), T. Hammond (E), Holt (M), Ivashin (M), Jones (E), Kapel (M), Kato (M), Kasuya (M), Klinowska (M), Leatherwood (E), Makeyev (I), McNamara (M), Mitchell (E), Nielsen (O), Ohsumi (M), Perdomo (M), Perrin (M), Quiroga (M), Sanpera (M), Shima (M).

Some participants did not attend all sessions of the meeting.

Perrin chaired the meeting and edited the report. Braham, Brownell, Collet, Gaskin, P. Hammond, Klinowska and Leatherwood served as rapporteurs.

The draft agenda was adopted after addition of an item 'Review of new information on other exploited small cetaceans' (Appendix 1).

2. REVIEW OF DOCUMENTS

Small cetacean documents (SC/35/SM1–34) submitted to the Scientific Committee are listed in Annex C of the main report. Also containing information on small cetaceans were SC/35/ProgReps Australia, Denmark, France, Iceland, Japan, New Zealand, Norway, UK, USA and USSR; IWC/35/11 and 19; SC 35/O 4; SC/35 PS1, 2, 3, 5, 6, 12, 15, 20 and 35; SC/35/Ba7; issues LXXXIX and XC (bound together) of the International Whaling Statistics and provisional statistics for catches outside the Antarctic in 1982.

3. REVIEW OF EXPLOITED POPULATIONS OF PHOCOENIDS

3.1 Harbour porpoise, *Phocoena phocoena*

The paper by Gaskin (SC/35/SM24) was used as the framework for the review of this species.

3.1.1 Population identity

The group agreed that the major divisions suggested by Gaskin (Bering Sea – North Pacific, North Atlantic and adjacent seas, and Black Sea – Sea of Azov) are undoubtedly separate. They also agreed that these 'regional populations' are likely composed of semi-isolated sub-populations such as those defined in SC/35/SM24 (Fig. 1), but that present knowledge in most cases is not adequate to allow delineation of boundaries between them. Sightings data do exist for some of the gaps indicated between the sub-populations, in the documents of this meeting (SC/35/SM5, 18) and in various unpublished data files; this information as available will be included in the final version of SC/35/SM24. It was also pointed out that hunting and sighting effort has been extremely low in some of the supposed gaps.

Also questioned was the inclusion in the ranges in SC/35/SM24 of deep-water areas, such as central Davis Strait and portions of the western Bering Sea. It was agreed that the harbour porpoise probably does not inhabit such areas, and the distribution map will be amended accordingly. Some other, minor range changes were suggested by members of the group and will be included in the revised map.

Gaskin reported that highly significant meristic and morphometric differences have been found between samples from the eastern and western North Atlantic, suggesting that these populations may be genetically isolated to a high degree (Yurick, 1977).

The group agreed that considerably more research will be necessary before most sub-populations can be adequately defined (see Recommendations) but that the sub-population units given in SC/35/SM24 provide a good provisional basis for review and planning.

Kapel informed the sub-committee that information on the occurrence of all small cetaceans, including harbour porpoises, is being collected at the Faroe Islands (Dorete Bloch, Museum of Natural History, Torshavn).

3.1.2 Population size

The sub-committee reviewed the tabulated estimates of population size in SC/35/SM24, area by area; in most cases no information was available. Some new documents and unpublished information were useful in providing updated provisional size estimates for other areas, e.g. Gulf of Alaska and Puget Sound, but no major changes were made.

The estimate for Washington to Southern California (600) was questioned because it is based on an aerial strip census. Gaskin reported that his research shows that the animals usually occur in small groups (commonly <5) and that they spend only about 7% of the time at the surface, diving and surfacing synchronously. This behaviour makes it likely that a significant proportion of animals may be missed in an aerial census, even directly on the track line. Also, as pointed out in SC/35/SM1, this species can be fairly easily confused with the Dall's porpoise under some circumstances. Both of these problems should be taken into consideration in designing a census survey.

3.1.3 Catches

Members of the group provided several corrections and additions to the catch data in SC/35/SM24 (for the Bering Sea, Gulf of Alaska, British Columbia, France, Greenland and Japan). Kasuya reported that harbour porpoises reported in SC/35/ProgRep Japan (and earlier progress reports) taken by harpoon in northern Japan were likely not harbour porpoises. More effort to identify animals taken is needed in that region.

It was noted that the 1,000–2,500 porpoise under 'incidental catches' for West Greenland in SC/35/SM24 have already been subsumed in the estimated directed take in the Danish statistics (the figure for directed take should be 500–1,500). Revised statistics for Greenland (1971–81) are provided in SC/35/SM19.

The takes by American Indians in the Gulf of Alaska are probably historical only; Braham reported that no catches have been observed or reported in recent years.

New data on incidental takes are included in SC/35/SM5 (northeastern Pacific and adjacent Arctic waters) and SC/35/SM14 (Danish fisheries, previously undocumented).

The sub-committee noted that substantial numbers of harbour porpoises (and porpoises of other species) die in gillnets in several types of fin-fish fisheries around the world (previous reports of this sub-committee). It is uncertain whether this indicates a special vulnerability or simply a conjunction of porpoise density and gillnets, but, in any case, research is urgently needed to investigate this special problem (see Recommendations).

3.1.4 Status

Very little information is available on the status of stocks of the harbour porpoise, but there is reason for grave concern in at least two areas.

(1) As reported in SC/35/SM14 and reviewed in SC/35/SM24, it is possible that a significant population decline has occurred in the Baltic – North Sea region. This may be due to pollution, disease, or by-catches. A decline may also have occurred along the coast of France (Duguy, Hussenot and Prieur, 1982). Andersen and Clausen (SC/35/SM14) reported a downward shift in overall size distribution and in distribution of size in sexually mature females between samples collected in a directed fishery in the early 1940s and samples from the by-catch in recent years. The group concluded that a shift in length at maturity seems unlikely, because a density-dependent response is usually manifested in a faster growth rate rather than in a smaller size at maturity. Gaskin reported that studies to compare ages in the two samples are underway. It was also noted that the different methods of capture (directed vs by-catch) may have resulted in differential age or size bias in the two samples. It is clear, in any case, that the population(s) may be in serious trouble and that assessment research should be continued and augmented.

The sub-committee notes that the coast of Norway could be of great importance as the eastern North Sea habitat of this species and suggests that scientists undertaking killer whale censuses in Norwegian waters be asked to extend their investigational scope to include *P. phocoena*.

(2) The other region of possibly serious depletion is the Black Sea. Knowledge of the fisheries and small-cetacean populations in the Black Sea were reviewed by this sub-committee last year (*Rep. int. Whal. Commn* 33: 152). In recent years, the bulk of the take by Turkey of several thousand animals annually for reduction to meal has been composed of harbour porpoises. The Turkish Government this year instituted a ban on any further take (see Item 6 below).

The situation in West Greenland is less clear. Some members of the group agreed with the tentative conclusion of SC/35/SM19 that the long series of stable by-catches since the 1930s (except for an increase in the late 1960s–early 1970s when a foreign salmon fishery operated off Greenland) indicates that the population has not declined. Other members, however, did not agree with this view. All agreed that the information necessary for an assessment of status (abundance, fishing effort, catch composition, vital rates) does not exist and that research would be necessary to obtain the information.

3.1.5 Recommendations

(1) Research is needed to define the populations. Member governments should be advised to sponsor comparative studies of morphology, parasite faunas, biochemistry/cytology, and reproductive parameters and seasonality. Collection of osteological specimens (with life-history information) from localities poorly represented in collections, such as Iceland, should be encouraged.

(2) As for other small cetaceans, more accurate and complete reporting of incidental take is needed. Member governments should be advised to upgrade their reporting system. For *Phocoena*, this is especially important for nations bordering the Baltic and North Seas and for the far-eastern nations.

(3) Member nations taking harbour porpoises incidentally in gillnets, e.g. Denmark (SC/35/SM14), should be advised of the preliminary results of experiments with anti-entanglement acoustical warning devices presently being tested for Dall's porpoise, *Phocoenoides dalli*, in the salmon gillnet fishery of the North Pacific (SC/35/SM28). This advice could also be offered to non-member nations with such a take, e.g. Canada (SC/35/SM5).

(4) Denmark should be advised to undertake research to collect data that will eventually allow assessment of the population(s) of harbour porpoises affected by fisheries in West Greenland.

3.2 Cochito, *Phocoena sinus*

The published account by Brownell (1983) was circulated. Brownell indicated that 26 specimens are now known. The status of the species is unknown, but since the fishery for *totoaba* (Sciaenidae) ceased, *Phocoena sinus* is no longer at risk from the extensive gillnetting for that species. The sub-committee noted that a series of recommendations for research had been made at the FAO meeting in Bergen 1976 but that little action has resulted other than two short-term surveys which made four sightings, none of which were confirmed (Villa-R, 1976; Wells *et al.*, 1981). The group agreed that a good abundance estimate is the primary requirement. At the very least, a survey of fisheries should be carried out to see if the animal is still being taken incidentally. This also could yield specimens from which data on life-history parameters could be obtained. Leatherwood reported that, as a result of diversion of flow in the Colorado river, the US Bureau of Reclamation will carry out extensive surveys in the delta region. The survey team could be alerted to watch for stranded specimens. Perdomo indicated that he will discuss the possibility of work on this species with staff of the National University (Mexico City). It was also noted that a workshop on the species will be held in conjunction with the 9th annual meeting on the marine mammals of Baja California to be held in March 1984 in La Paz, B.C., Mexico.

3.3 Spectacled porpoise, *Phocoena dioptrica*, and Burmeister's porpoise, *P. spinipinnis*

The sub-committee had no new information on the latter, but were informed by Cawthorn that an article in press by E. Fordyce contains a range extension for *P. dioptrica* to MacQuarie Island, Australia. Nothing is known of population identity, size or status for these species. *P. spinipinnis* is taken in nets on the west coast of South America, but catch statistics are not available (Brownell and Praderi, 1982).

3.4 Dall's porpoise, *Phocoenoides dalli*

3.4.1 Population identity

The most recent work on this question is that of Kasuya (1978 and 1982) for the western North Pacific. He identified three populations: a 'Sea of Japan – Okhotsk Sea population', an 'offshore western North Pacific and Bering Sea population' (involved in the high-seas salmon gillnet fishery—SC/35/SM8), and a 'Japanese east coast population' (the object of a land-based harpoon fishery in Japan). These divisions are based mainly on the relative frequencies of two colour morphs called 'dalli-type' and 'truei-type'.

Braham presented unpublished distribution data for the entire North Pacific obtained from vessels of opportunity (supplementary to the data in SC/35/SM18). There are no obvious gaps in distribution that might indicate existence of sub-populations within the overall offshore North Pacific and Bering Sea range. There are sightings for all areas of sighting effort. While uneven effort coverage (SC/35/SM12) complicates the picture, the species appears to be less abundant in the Bering Sea.

Studies to examine stock identity are underway at the US National Marine Mammal Laboratory, at Ehime University and at the Ocean Research Institute, University of Tokyo. These are based on comparative skeletal morphology, parasite faunas, pollutants and isoenzyme analyses. Members of the group suggested that the research might be broadened to include studies of mitochondrial DNA and pigmentation.

3.4.2 Population size

Alternative estimates of population size for the entire offshore North Pacific were presented in SC/35/SM12 and 27. It was noted that both are based on pelagic observations and that no new estimates are available for Japanese waters. The Bouchet estimate (790,000 to 1,738,000—SC/35/SM12) was based on surveys involving only trained observers, while only some of the observers used in the surveys yielding the Kato estimate (1,500,000 to 2,300,000 by the line-transect method—SC/35/SM27) received prior training in identification and sighting methods. Kasuya reported that while a Doi-method estimate was also presented in SC/35/SM27, the analysis uses parameters that should be adjusted for both typical behaviour of the animals and searching habits of the observers. This was not feasible in the present case.

Jones reported that while the estimate in SC/35/SM12 is a strip-census estimate, future analyses may employ the more generalized line-transect method. The group noted that the Kato estimate involves extrapolation to an area about 20% larger than that involved in the Bouchet estimate, accounting for much of the difference between the estimates. Several problems with the Kato estimate were pointed out. The Fourier series is not necessarily the best model to fit to a distribution of perpendicular distances which is spiked close to the transect line and may result in underestimation of abundance in this case. The estimate of variance of density of groups ($V(D_g)$, SC/35/SM27) is likely an underestimate because of the implicit assumption that groups are randomly distributed. Judging from the data in SC/35/SM12 and 18, this would appear to be unjustified. Effort was unevenly distributed because of the nature of the sample, possibly leading to a bias in the estimate. This could be avoided by stratifying the range in such a fashion that survey effort is uniformly distributed in each stratum. The group discussed the effect of adverse sighting conditions. Although the Bouchet analysis used only sightings made at Beaufort-4 conditions or better, the effect of weather (described in SC/35/SM10) may still have been to cause an underestimation of abundance, because the strip-census method assumes that all animals within the strip are seen.

The group also discussed the problem of attraction of cetaceans to survey vessels. If Dall's porpoises approach vessels more than they avoid them, then the line-transect method can be expected to yield overestimates of abundance. In an experiment involving observations from a helicopter (SC/35/SM13), animals approached the vessel more often than they moved away from it, but the results were inconclusive because of small sample size. To complicate things further, the results presented here (SC/35/SM10) indicate that there may be geographical and seasonal variation in the way this species reacts to ships. The group agreed that this is a paramount problem that must be solved before the line-transect method can be used with adequate confidence.

Another problem with the estimates is that both involve extrapolation to very large areas that have received very little or no survey effort. This can lead to extreme error, most likely in the direction of overestimation, and should be taken into account in making use of the estimates. Jones and Kasuya both stated that data collection and analyses are continuing.

3.4.3 Catches

The sub-committee examined document SC/35/SM28, listing the reported incidental take since 1978 in the land-based and mothership salmon drift-net fisheries, and SC/35/SM8 on the estimates of the take based on data collected by observers and the mothership fishery. Kasuya provided summaries from Japanese progress reports on take since 1963 by the Japanese coastal harpoon fishery.

The sub-committee noted with concern that the 1982 catch by the harpoon fishery boats was 12,833 animals, an increase of 3,030 from 1981 and the largest directed catch ever made in this fishery. It was suggested that the increase was a result of some boats staying at some distance from port for longer periods to economize on fuel. Another possible reason is a decrease in the drive-in catch of striped dolphins, *Stenella coeruleoalba* (from 4,783 in 1981 to 1,994 in 1982—SC/35/ProgRep Japan and *Rep. int. Whal. Commn* 33:213–20).

Odate and Ito presented statistics on the reported kill in the mothership salmon gillnet fishery (SC/35/SM28) of 1,000 for 1980, 1,361 for 1981 and 3,190 for 1982. These are lower than the estimates of incidental take based upon observer data presented by Jones (SC/35/SM8) of 8,970, 2,862 and 5,903.

Upon discussion, it was agreed that the doubling of kill from 1981 to 1982 most likely reflects a shift in distribution of areas of high porpoise density or shifts in fishing areas, because fishing effort did not change substantially.

Balcomb reported that there is an unreported incidental catch of Dall's porpoises in gillnets in Washington State, USA.

3.4.4 *Vital rates*

The sub-committee noted that the available data for the pelagic drift-net catches show a very high annual pregnancy rate (90–95%) and that age-determination studies point to a much lower age (3.3 years in females) at attainment of sexual maturity than was found by Kasuya (6.8 years—1978) in the inshore harpoon fishery samples. The important question to be asked is if these are real characteristics of the population, or artifacts due to biased catches or significant segregation by age or sexual condition. SC/35/SM10 suggests that some segregation does occur. The authors concluded that (1) females in the state of late pregnancy, lactation, or pregnancy and simultaneous lactation are mainly distributed in the northern part of the area surveyed, and that (2) the southern part of the area is mainly occupied by males and some few females not accompanied by calves. This result indicates that not all females become pregnant every year. The predominant calving interval appears to be one year, implying a relatively high gross reproductive rate. Concerning age at attainment of maturity, Jones reported that research continues on the age-determination method and that the samples are being re-analyzed. In addition, large samples from 1981 and 1982 have not yet been examined.

The sub-committee also discussed the drop in pregnancy rate coincident with increase in lactation rate and number of corpora albicantia (SC/35/SM9, Table 7). A change in breeding season or lower fecundity with age and higher pregnancy rates in females which have matured in the last few years were discussed as possible contributing factors, but no conclusions could be drawn at this time. Jones reported that research on this question continues.

Males in the population involved in the salmon fishery attain sexual maturity at 5–6 years (maturity is reached at 8.1 years on average in the Japanese population—Kasuya, 1978). Length of gestation and lactation are not known but are thought to be relatively short (SC/35/SM9).

3.4.5 *Status*

According to SC/35/SM28, an increase in catch-per-unit-effort over the last 20 years suggests an increasing population. Kato (SC/35/SM27), however, thinks that the annual variation in his population estimates is due to incomplete coverage of the research area. It was also noted that the CPUE figures for the research vessels were based on a very small number of animals taken each year. The group agreed that the data do not provide evidence of an increase in abundance. Jones reported that the last assessment of status by the USA was in 1981, based primarily on data from 1978 and 1979. A new assessment will be carried out in early 1987. The 1981 assessment assumed a net recruitment rate like that of *Stenella* spp. in the eastern tropical Pacific, which have calving intervals of roughly two years. It also assumed a catch of one animal per net set, which is at the high end of the recorded range of values. The assessment is thus conservative with regard to these factors. The very important question of stock identity, however, remains unresolved.

Kasuya reported that complete effort data are not available for the harpoon fishery off Japan and that the status of the porpoise population there is unknown. Collection of biological specimens from the fishery has begun.

3.4.6 *Gear research*

Vessels using experimental acoustic devices (hollow monofilament line or pingers attached to the nets) have reported a 40% reduction in incidental kill of porpoise (SC/35/SM28), but evaluation of the data is in progress. Jones reported that under agreement between the USA and Japan, 25% of mothership-fleet vessels fishing in 1984 will be required to employ the devices. Fifty percent must be equipped in 1985 and 75% in 1986. Experimental work with pingers of various frequencies and hollow-line nets continues, as do efforts to record the sound emissions of Dall's porpoise at sea and in captivity. Doubts were expressed by some members of the group about high-frequency (c. 140 KHz) generators in such work because of (a) the rapid attenuation and (b) possible attraction to the devices. Others, however, felt that the latter was unlikely to be a serious problem.

3.4.7 *Recommendations*

(1) The studies to examine population identity should be broadened and given high priority and the research on attraction to vessels continued.

(2) Considering the large and increasing take by harpoon, Japan should be advised to institute a system for collecting effort data and to carry out a sighting survey to estimate abundance.

(3) The Soviet Union should be advised to analyse and make available sightings data from the Kurile Islands area of the Sea of Okhotsk (the porpoises that are fished off Japan migrate to Soviet waters in the summer).

3.5 Finless porpoise, *Neophocaena phocaenoides*

No significantly new information on this species was available to the sub-committee. Kasuya noted that the statistics on incidental catches by fishermen in the Inland Sea are not presently fully reported in the Japanese Progress Reports because specimens are discarded rather than taken to the markets. Two live-captures were noted in Java (SC/35/SM2). Almost nothing is known of population identity, size or status. Semi-isolated riverine populations may exist.

The sub-committee agreed that any research or baseline data collection would be useful since so little is known about this species. Member nations, for example India and the People's Republic of China, should be encouraged to collect catch statistics and make them available to the Scientific Committee.

4. REVIEW OF POPULATIONS INVOLVED IN LIVE-CAPTURE FISHERIES

The Committee reviewed documents available to it on live-capture fisheries (SC/35/SM2, 3, 4, 5, 14, 22, 26, 29, 30, 31, 32 and SC/35/ProgReps Iceland and USA). Authors present briefly reviewed the methods, findings and limitations of their contributions. Data on live captures by species and area are summarized in Appendix 3.

Data on catches for aquariums in Indonesia (SC/35/SM26) and Hong Kong (SC/35/SM3) were summarized directly from institution records and are regarded as accurate for the approximately one decade each has existed.

Reporting by the USA is probably close to complete for the years since 1972, but the coverage for earlier years is piecemeal (SC/35/SM4).

Records for Japanese live-captures are similarly regarded as more complete after 1973 (SC/35/SM26).

Reports of takes for European institutions are incomplete, as they are based on partial response to questionnaires. Only 36% of the institutions and individuals queried responded (SC/35/SM29). In several instances minimum takes known from publications or other sources were difficult to reconcile with the takes reported.

Data reported for South America are only minimum estimates of removals by live capture for two species (*Inia geoffrensis* and *Sotalia fluviatilis*) no longer sought in appreciable numbers, but listings are thought to be complete for *Cephalorhynchus commersonii*, in which there may be increasing interest (SC/35/SM30).

Records for New Zealand institutions reportedly lack only a few reports by attending veterinarians concerning previous holdings of several smaller institutions now closed (SC/35/SM32). Data presented for Australia reflect only present holdings (SC/35/SM32) and do not include at least one specimen of *Orcaella brevirostris* known to have been held at Cairns and possibly also individuals of other species held previously. Although there is no central system of recording live-captures for Australia, more complete information on past catches could be obtained from state governments and the institutions themselves.

For South Africa, where records have been required since the initiation of the fishery in 1961, there are good data available on all 59 specimens live-captured. Animals previously were housed at commercial aquariums (2) or research oceanariums attached to institutes (2), but present holdings are distributed, as a policy decision, only at the latter (Ocean Research Institute in Durban and Port Elizabeth Museum) rather than at commercial aquariums, and export is now prohibited.

In reviewing the live-capture data and possible impacts on populations, the group agreed to include only live and 'healthy' animals removed from the wild (through deliberate live-capture, drive fisheries, or accidental entanglement/entrapment) and to ignore stranded cetaceans recovered from the beach, regardless of their subsequent captive histories.

Captive births have been reported for *Tursiops truncatus, Grampus griseus, Orcaella brevirostris, Phocoena phocoena, Neophocaena phocaenoides, Inia geoffrensis, Orcinus orca* and *Stenella longirostris.*

After a brief review of the 32 species known to have been collected live, the group agreed to focus on 16 species for which the combined factors of stock identity, population size and status, takes (including all directed and incidental takes) and legal status and management seem to justify more intensive review. The sub-committee then broke up into four sub-groups which collated, examined and summarized information on the 16 species in the meeting documents and in the available literature. The full sub-committee then reviewed the results of this exercise and pared the list of species down to 5 for which concern and recommendations would seem to be justified in the case of one or more populations:

killer whale, *Orcinus orca*;
bottlenose dolphin, *Tursiops truncatus;*
short-finned pilot whale, *Globicephala macrorhynchus;*
tucuxi, *Sotalia fluviatilis;*
Commerson's dolphin, *Cephalorhynchus commersonii.*

4.1 Killer whale, *Orcinus orca*

4.1.1 Population identity

Killer whales occur worldwide with greatest abundance within 500nm of shore in cold waters of both hemispheres to the polar ice caps. Stocks in each ocean are presumed separate and distinct. For at least inland marine waters of Washington and British Columbia, there is good evidence for a high degree of isolation of coastal populations, suggesting that broader-scale units as used for larger species may be inappropriate for killer whales (*Rep. int. Whal. Commn* 32: 117).

Live captures have been made in or are planned at present for only 5 areas (in Washington, British Columbia, Alaska, Japan and Iceland), which can be presumed to be parts of ranges of populations that are separate and distinct from one another.

4.1.2 Population size

SC/35/SM7 presents data on present day killer whale distribution and abundance in Southeast Alaska (from Alaska Trollers Association logbooks, 1976–1982), Prince William Sound (from surveys 1976–78, vessel surveys 1976/1981), Shelikof Strait (from surveys, 1982–83). Data for all these areas were also collected through interviews. Minimum counts are 93, 80 and 66, and minimum estimates are 93, 100 and 100 for the 3 areas, respectively. A minimum count of 284 has been made for Iceland (SC/35/SM31 discussed below in Item 7) and an estimate of 303 made for British Columbia (Bigg, Macaskie and Ellis, 1983). There are no estimates for populations in Japanese waters.

4.1.3 Catches

Live capture of this species for display commenced in 1964 with a male taken in British Columbia. From 1964 to 1976, approximately 58 animals were removed from inland marine waters of Washington/British Columbia for exhibit (Bigg and Wolman, 1975; Asper and Cornell, 1977). A few additional whales died in capture operations. Others were captured and released. There is no other known exploitation of the population in these areas. Live-captures in Japanese waters began in 1973. Through 1982 a total of 9 animals had been removed (SC/35/SM26). Killer whales in Japan formerly were taken for human or animal food and for oil and by-products. Ohsumi (1975) reported catches of 1,477 from 1948 to 1972, and Miyazaki (1982) reported takes of 12 from 1976–1981, of which 10 were caught in drive fisheries and 2 by small-type whaling. Some of these were taken to aquariums. The species continues to be taken in small numbers in drive fisheries (4 in 1982), and fixed nets (1 in 1982) (SC/35/ProgRep Japan).

Since they began in 1976, live-capture operations in Iceland have resulted in removals of 39 animals; two died in captivity in Iceland and 37 were exported. An additional 7 were captured but released (SC/35/SM31; Sigurjónsson, 1983). Icelandic populations formerly were exploited by a Norwegian fishery which took 300 animals from Icelandic waters (many well offshore) between 1955 and 1972 (Jonsgård and Lyshoel, 1977; Christensen, 1982), while between 1955 and 1960, killer whales were the target of kills to reduce competition with the herring fleet. Total kills in this effort are unreported.

4.1.4 Status and management

Nothing is known of the status of killer whale populations involved in live-capture operations.

The United States Marine Mammal Protection Act of 1972 requires that all 'takes' of cetaceans in US waters, including live-captures, be authorised by permit. No such permit has been issued for the taking of killer whales since 1976, but Perrin reported that one application is pending for 'removal' for live maintenance of up to 10 whales from Alaska over 5 years and encirclement, handling and release for scientific study of up to 90 whales off Alaska and California over 5 years. A permit system for live captures also exists in Canada, where 1 permit was issued in 1983 to take 2 killer whales from British Columbia for exhibit. That permit has been retained unused, as three whales were requested to be imported from Iceland in May 1983. A permit system for live-captures also exists in Iceland, where 15 permits have been issued for the taking of a total of 62 whales (SC/35/SM31).

Considering the relatively low levels at which killer whales have been exploited world-wide, the species cannot be considered endangered. However, to the extent that stocks are localized and isolated, any exploitation of them can be expected to have long-term impacts on population size and structure (*Rep. int. Whal. Commn* 32: 59). Because of the possibly very low rate of reproduction in this species in at least some populations, if a guideline for rate of removals is adopted pending stock assessment, as has been done by the US (see *Tursiops* below), it should probably be lower than the annual rate of 2% that has been used for *Tursiops*.

4.1.5 Recommendation

Mindful of the probability that populations in a given geographical area consist of localized stocks, the sub-committee recommends that any planned live-captures by the USA, Iceland and Japan or elsewhere be preceded by an assessment of size and composition of the populations to be affected.

4.2 Short-finned pilot whale, *Globicephala macrorhynchus*

4.2.1 Population identity

The species is distributed world-wide in tropical and lower-latitude temperate waters, but live-captures are reported only for the North Pacific (SC/35/SM4, 26). Mitchell (1975, ed.) reported indications that there are two forms in the North Pacific (defined during the meeting by Kasuya for Japanese waters as a larger northern and a smaller southern form) and said that both are probably fished off Japan.

4.2.2 Population size

There are no published estimates of population size for the North Pacific, but the species is not considered rare.

4.2.3 Catches

This has long been a popular display animal in the United States (SC/35/SM4). Twenty animals were caught off Hawaii between 1963 and 1972. All 17 catches since 1972 and undetermined numbers live-captured between 1966 and 1972 (including at least 33 (Walker, 1975) but thought to total 50–100 animals — reported by Leatherwood) were from Californian waters. Perrin reported that tens of animals were taken annually in gill nets and round-haul nets off Southern California. Research toward an assessment of this population is in progress.

In the Western Pacific the species has been taken for live display from the drive fishery at Taiji, Japan, which has operated sporadically since at least the mid-1960's but has kept data on live removals only since 1969. From 1969–1982 the total commercial and incidental take, from Taiji and elsewhere, was 3,009 (Miyazaki, 1983, p.624; SC/35/ProgRep Japan), including small numbers of the larger form taken by small-type whaling (reported by Kasuya).

4.2.4 Status and management

There is no indication that the low levels of removal off California have affected the species there, but the population has not been assessed. Japanese live captures are unlikely to have a significant effect on the population(s) by themselves, given that they represent only about 2% of the mean annual catch from 1973 to 1982 and about 5% from 1976 to 1982 (SC/35/ProgRep Japan and SC/35/SM26), but members of the sub-committee expressed concern about the size of the aggregate catch given that the population has not been assessed. Kasuya reported that maximum catch limits are set by local governments.

4.2.5 Recommendations

(1) In view of the aggregate catch of the small form in Japanese waters, Japan should be advised to assemble available information and data relevant to a possible assessment and make the material available to the Scientific Committee for review.

(2) The USA should be encouraged to make a progress report on its assessment of eastern North Pacific population(s) available to the Scientific Committee.

4.3 Bottlenose dolphin, *Tursiops truncatus*

4.3.1 Population identity

The species is found world-wide in temperate and tropical waters, near-shore and offshore. In most areas studied there is a smaller form and a larger form (Mitchell, ed., 1975), although distinctions between them are not well described. From detailed studies of local populations involved in US live-capture fisheries (Odell and Asper, 1982; Asper and Odell, 1980; SC/35/SM22) it is clear that at least coastal animals are distributed in populations occupying separate but overlapping sections of ocean coastline and associated inland marine waters. Live-capture operations conducted to date in most areas have exploited such coastal populations.

4.3.2 Population size

Although the species appears common in much of its range, there are estimates of numbers available for only one region in which live captures occur at present. SC/35/SM22 presents estimates for sub-populations/management units of the southeastern USA obtained from systematic or random aerial surveys using strip or line-transect techniques. Estimates of sizes of regional/local populations range from 35 (Apalachicola/St. Joseph Bays) to 1,342 ± 847 (Mississippi, Chandleur and Breton Sounds).

4.3.3 Catches

In terms of numbers of populations from which animals are collected and total takes world-wide, this is the most important species of cetacean to live-capture fisheries.

Live-captures in many areas (e.g. Australia, Mexico, New Zealand, Indonesia and the Mediterranean) have involved small numbers over relatively long periods, but from the United States an estimated minimum of 1,595 to 1,635 dolphins of this species (1,578–1,613 from the southeastern USA) have been taken since 1914 (Leatherwood and Reeves, 1982; SC/35/SM4). Although there are no other takes reported for US waters, wherever the species occurs sympatric with net fisheries around the world some incidental mortality takes place and such kills can be supposed to occur in the USA.

In Japanese waters, a total of 580 dolphins of this species has been taken for live display since 1974 (SC/35/SM26). Most (93%) were taken from drive fisheries at Taiji and Iki or from incidental catches by other fisheries. The remainder were intentionally sought and captured by aquarium staff or contracted fishermen/collectors. In addition to the live captures, in 1982 alone, 834 were reported killed in drive fisheries and fixed nets (SC/35/ProgRep Japan). Miyazaki (1982) reported that a total of 6,827 dolphins of this species were taken between 1976 and 1981 (ave = 1,138), by driving (6,350), set net (254), harpoon (213), and small type whaling gillnet (10).

Though numbers reported taken by live-capture off Australia are low (28 +), there may be some additional mortality in shark nets in the same areas where live capture takes place (Paterson, 1979).

The sub-committee is aware of additional unreported live captures of this species from the Black Sea, the southeastern Philippines, the South China Sea, the Strait of Malacca, and Western Malaysia.

4.3.4 Status and management

Although there is at present no basis for concern that live-capture fisheries have had a detrimental effect on the species overall, there is concern that in the long term, sustained takes from localized populations may have had significant impact. The sub-committee notes the US government's committment to an interim management programme, in which population numbers are being estimated for regional stocks/management units and takes of no more than 2% of the minimum estimated population per year are being permitted in each stock (SC/35/SM22).

Leatherwood reported that increasing numbers of this species are born alive at oceanariums and can, in the future, be expected to reduce the burden on free-ranging populations to supply captive needs.

4.3.5 Recommendations

(1) The sub-committee feels the guideline for takes pending stock assessment of 2% per year to be prudent and believes that it can be safely followed pending results of other assessments. It recommends that continuation of research on stock identity by the US be encouraged, and that population census and interim management procedures be initiated for on-going or planned live-captures of this species elsewhere.

(2) In view of the aggregate take of this species in Japan, the sub-committee recommends that Japan be advised to at least determine the stock identity and abundance of the populations impacted.

(3) The sub-committee recommends that the Australian government be advised to make an effort to identify to species the small cetaceans taken incidentally in anti-shark nets and include the information, as well as live-capture data, in its progress report to the Scientific Committee.

4.4 Tucuxi, *Sotalia fluviatilis*

4.4.1 Stock identity

At least two separate populations exist, one freshwater and the other coastal marine. The coastal marine dolphins are larger than the freshwater animals. Nothing is known about populations within the river systems or along the coast.

4.4.2 Population size

No data are available.

4.4.3 Catches

Since the mid-1960s over 45 dolphins have been taken from South America (mainly Colombia) in the live-capture fishery. A small number were also taken live in Brazil. No incidental catches are known from Colombia. Recent incidental catches are known from Brazil (Best and da Silva, in press).

4.4.4 Status and management

Nothing is known about the status of this species. It is listed in Appendix 1 of CITES. The European nations into which the animals have been imported are parties to CITES and must issue permits for import. Colombia, the principal nation of export, is also a party to CITES.

4.4.5 Recommendation

Brazil should be advised to collect, and provide in its progress report to IWC, statistics on the number of dolphins taken incidental to other fisheries and to collect information on basic life-history parameters from these animals.

4.5 Commerson's dolphin, *Cephalorhynchus commersonii*

4.5.1 Stock identity

This species is found in coastal waters of Argentina from Peninsula Valdes (*ca* 42°05'S) to southern Tierra del Fuego and the Strait of Magellan; it is also found around the Falkland Islands, South Georgia and Kerguelen Islands. The island population(s) are certainly separate from one another and from those on the coast of Argentina. Coastal populations appear localised, for example near river mouths.

4.5.2 Population size

Estimates are unavailable.

4.5.3 Catches

Since 1978, a total of 24 animals have been taken from Argentine waters in the live-capture fishery (20 from Commodoro Rivadavia and Puerto Deseado). No incidental catches are known from the regions of capture.

4.5.4 Status and management

Status is unknown.

4.5.5 Recommendations

The demand for live specimens, most likely from Argentine waters, will probably continue. Argentina should be advised to monitor removals by capture area (because of the apparently localised coastal populations) and to review coastal fisheries to determine if there is an incidental take. Carcasses should be salvaged to provide basic life-history data and specimens.

5. REVIEW OF NEW DATA AND ANALYSES FOR BAIRD'S BEAKED WHALE

At the meeting of the Scientific Committee in 1982, the sub-committee reviewed an analysis of catch and sightings data concerning the Japanese coastal fishery for Baird's beaked whale. The sub-committee expressed concern that the catch-per-unit-of-effort analysis could not be evaluated because the nature of the fleet had varied over the period of analysis and that the hiatus in scouting boat sightings data off the coast of Japan might indicate more than one stock. The sub-committee recommended that the catch and sightings data be reanalysed to take account of the problems with effort, that the scouting vessel sightings data be reanalysed to try to determine stock ranges, that additional research be carried out to determine stock ranges, possibly by use of aerial surveys or tagging, and that population dynamics be investigated.

The government of Japan set a national quota of 40 whales for the 1983 season. The catch in 1982 was 60 whales, 21 more than in 1981.

This year, the sub-committee was pleased to receive document SC/35/SM25 describing a re-analysis of the catch and sightings data and to note that there are two Japanese sighting and tagging cruises using Japanese tags taking place this year in June–August with Baird's beaked whale the primary target and that aerial survey data collected from coastal waters in previous years will be reanalysed.

Kasuya summarised SC/35/SM25, noting that the operational record of the fleet has been analysed over the period 1947–1982, that the sightings records from scouting boats had been re-analysed by month, and that a detailed analysis of the data for Area D had been done for 1977–1982. SC/35/SM25 showed that a regression of catch/boat/month for July and August on year from 1947 to 1982 was not significantly different from zero for fishing vessels of less than 40 gross tonnes, greater than 40 gross tonnes or for the combined data using a correction ratio to account for vessel size. The sub-committee noted that there is yearly variation in the length of the fishing season within these two months and that this introduces variability into the CPUE series which could possibly be masking a trend. However, there are no data on dates of beginning and end of fishing within the first and last months of the season, respectively, prior to 1977. On the question of correcting the data for the marked increase in vessel size from 1947 to 1974, the sub-committee noted that it would be useful to investigate the data for 1965–68, the only period of appreciable overlap in the operation of the smaller and larger vessels. Two separate analyses of the catch-per-month data for the six vessels operating during this period were carried out by Holt and by Kasuya and Miyashita. The sub-committee was unable to resolve the different results and conclusions of these analyses, and concluded that analyses of more detailed data were necessary. Holt stated that he considered the CPUE analysis in SC/35/SM25 to be methodologically invalid. The sub-committee noted that the more detailed data available in recent years showed no trend in sightings per operational hour from 1977 to 1982.

SC/35/SM25 concluded, based on changes in the distribution of sightings from scouting boats from month to month, that the range of Baird's beaked whales found in Japanese coastal waters was probably continuous with that of the animals seen in the rest of the North Pacific but that further study was needed. The sub-committee considered that the effort expended by the scouting boats in the waters off the coast of Japan was insufficient to draw any firm conclusions. The results from the Japanese sightings cruises this year may provide information which could help to resolve this problem.

Ohsumi and Kasuya stated that Baird's beaked whales were only taken by small vessels, certainly within 200 miles of the coast. Ohsumi also noted that the increased effort and resulting high catch in 1982 was probably a response to an increased demand for whale meat in Chiba (adjacent to Area D).

In conclusion, the sub-committee noted that there are still problems with measurement of effort precluding an evaluation of data currently available for 1947–1976, and that detailed data on catch/boat/month for each fishing vessel in each year are required in order to resolve this problem. In addition, the sub-committee noted that the questions of stock identity and range are unresolved.

Recommendations

The sub-committee recommends that research on effort measures and stock identity continue and that the available effort and catch data by boat and by month be made available to next year's meeting of the Scientific Committee.

6. REVIEW OF NEW INFORMATION ON BLACK SEA DOLPHIN AND PORPOISE POPULATIONS AND FISHERIES

The Turkish Government has issued a decree banning dolphin and porpoise hunting in the Black Sea starting in mid-April, 1983, for at least one year. Rifles and ammunition used in the hunt are being confiscated.

The sub-committee reviewed the Black Sea populations and fisheries last year and made several recommendations, some of which have been acted on. The recommendations and present status (in parentheses) follow. The group recommended

(1) that improvement in harvest statistics be made, with the help of FAO (FAO this year sent a general fishery mission to Turkey which among other activities procured information on the dolphins and porpoise);

(2) that the USSR make available data from its aerial sighting surveys in the eastern Black Sea (the data have not yet been made available);

(3) that Turkey be invited to send a scientist to this year's meeting of the Scientific Committee (Turkey was invited to send a scientist to this year's meeting, but did not accept the invitation, possibly because of funding problems);

(4) that the history and present status of the anchovy fisheries be investigated and the results made available to the Scientific Committee (no new information is available on the anchovy fishery); and

(5) that the catch of dolphins and porpoise be sampled to determine sex and size composition and reproductive condition of the animals (a research programme is to be initiated with advice and funding from international sources — informal FAO source).

The FAO mission obtained catch statistics for the three species in the aggregate for the period 1976 through 1981.

Year	Catch (mt)	Ave wt. (kg)	Est. no. individuals [1]
1976	1,590	40.6	39,162
1977	2,608	38.4	50,822
1978	1,907	36.4	52,390
1979	1,827	38.5	47,450
1980	2,721	53.3	37,150
1981	886	41.7	21,247
Total	11,539	—	248, 221 (Ave. 41,370)

[1] Catch in tons divided by ave wt.

An independent estimate of average catch during the period was based on consumption of rifle ammunition in the hunt. About 103,000 to 133,000 rounds were used annually. The dolphin hunters claim that about 1 shot out of 3 kills a dolphin. This implies an annual kill of about 34,000 to 44,000, a range that brackets the 10-year average estimate based on catch in tons (informal FAO source).

Recommendation

The sub-committee recommends that the scientist in charge of the Turkish research programme be invited (and funded by IWC, if necessary) to participate in the next meeting of the Scientific Committee, to present a progress report and to discuss plans for future research.

7. REVIEW OF NEW INFORMATION ON OTHER EXPLOITED SMALL CETACEANS

Because of the shortage of time due to major concentration on live-capture fisheries, review of Baird's beaked whale, and the review of exploited populations of phocoenids, the sub-committee only briefly reviewed new data on other small cetaceans, with the exception of the incidental catch of small cetaceans off Australia and killer whales.

7.1 Incidental catch of small cetaceans off Australia

Information on incidental catch of small cetaceans in a gillnet fishery for shark, tuna and mackerel in Northern Australian waters is summarised in SC/35/SM21. Gillnetting by vessels from Taiwan started in 1974. With the declaration of the Australian Fishing zone in November, 1979, the fishery came under Australian control, and Australian observers started to gather incidental catch data in 1980. The estimated total cetacean by-catch, including *Tursiops truncatus*, *Stenella longirostris*, *S. attenuata*, and *Pseudorca crassidens*, between June 1981 and February 1983 is 4,463 ± 1,550 animals. A linear-regression analysis of cetacean-catch rate against cumulative fishing effort shows a significant decline in catch rate over the 21-month period considered.[1] McNamara reported that plans are underway to study the incidental take in this fishery and collect biological specimens.

7.2 Killer whales

P. Hammond summarised data in SC/35/SM17 on the density and number of killer whales in Antarctic Areas II, III, IV and V surveyed by the IWC/IDCR Minke Whale Assessment Cruises using line-transect sampling methods. In the area surveyed, the overall density and total number of killer whales was estimated to be 81 whales per 1000 sq. nm and 163,500 whales, respectively. Estimates for Areas III and IV supported Allen's (1981) opinion that his estimate was probably too high and that Best's estimate was probably too low. The estimates in SC/35/SM17 differ from those previously presented primarily in three respects. Firstly the data were 'smeared' in an attempt to reduce bias caused by rounding sighting angles to convenient values, particularly zero degrees; secondly, a more appropriate model was fitted to the data, and, thirdly, analyses showed that the data did not need to be stratified by area.

The sub-committee reviewed the data presented in SC/35/SM31 on killer whale sightings off Iceland during October 1982. Sigurjónsson attempted to determine the minimum number of killer whales present on the Icelandic herring grounds by distributing specially designed recording forms to fishermen. The highest 'minimum number' of killer whales was 284 animals on 15 October, 1982. The author suggested that the 'minimum number' is conservative, as only a small part of the Icelandic coastline was covered and the herring fishery occurred mainly within 10 nm of the coast. The author used 15 nm as the minimum distance between vessels on the same day before data were disregarded. Leatherwood noted that to obtain a count for a given day, in his survey (SC/35/SM7), the largest number in one area was used as a starting figure and that further sightings on the same day were only added if they were made at least 110 nm away. This is the longest estimated distance moved by any of 30 herds of killer whales tracked in Puget Sound (Balcomb, 1978).

7.3 Dolphins impacted incidentally by fisheries

A paper was available that was prepared for the annual meeting of the Standing Committee on Research and Statistics, International Commission for the Conservation of Atlantic Tunas (Coan and Sakagawa, 1983). The authors noted that the US tuna purse-seine fleet has operated in the Atlantic ocean since 1967. Major emphasis was on analysis of data from the eastern tropical Atlantic for the period 1967–1980. Dolphin sets were rarely made by US vessels operating in the eastern tropical Atlantic. The largest number of dolphin sets in one year was 26, off Liberia in 1967.

Hammond's paper SC/35/SM16 on dolphin mortality incidental to purse-seining for tunas in the eastern tropical Pacific for 1982 was noted but not discussed.

Notes on small cetaceans observed during an IWC/IDCR cruise in the eastern tropical Pacific were contained in SC/35/SM23.

Quiroga reported that the Spanish Institute of Oceanography has initiated an enquiry on the fleet of vessels that fish for tuna. The goal of this inquiry is to determine the extent of incidental capture of small cetaceans and the species captured. The first information collected is for the vessels that use nets. The fleet that uses trolling gear and live bait does capture some dolphins, which are used for food. It is still too early to estimate the quantity of these captures.

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[1] Editor's note. Since the meeting this paper has been revised. The revised catch for June 1981–March 1983 is 4,577 ± 1,331. Linear regression analysis over this period reveals no significant decline. However if the 22-month period June 1981–March 1983 is examined (catch 4,662 ± 1,403) the decline in catch rate is significant.

Records of pelagic dolphins in the Northern Indian Ocean Sanctuary, including incidental takes in net fisheries off Sri Lanka, were noted in SC/35/SM6.

7.4 White whales

SC/35/SM20 dealt with white whale distribution and migration in the Kara Sea but was not discussed.

7.5 Bottlenose whales

A paper on the history of the bottlenose whale fishery in the North Atlantic was available (SC/35/SM15) but was not discussed. Christensen reported that an expanded version will be submitted to the Committee next year.

8. OTHER BUSINESS

8.1 Takes of small cetaceans in 1982

Information on takes (directed, incidental and live-capture) available in the documents of the meeting or provided by participants is summarised in Appendix 4.

8.2 New information on the effects of pollution and industrial development

The progress reports of Australia, Denmark, France, Japan, New Zealand, Norway, Spain, USSR, UK and USA and papers SC/35/SM3, SM14, O 13, IWC/35/11A and 11E contain information on this subject. The Committee, however, was disappointed to note, yet again, that most information relates to levels of contaminents and not to possible effects. Only Australia, Denmark, France, USA and Canada appear to have such work in progress.

The 1982 ICES meeting reviewed the effects of pollution on marine mammals (IWC/35/11A). It was concluded that the levels of pollutants observed vary greatly with age, sex and location and that effects are complicated by interactions between direct metabolic effects and environmental interactions. Since no firm conclusions could be reached at that meeting on the effects of pollutant burdens on reproduction and survival of marine mammals, this will be a special topic for the 1983 meeting.

The FAO/UNEP Consultation on the Global Plan of Action for the Conservation, Management and Utilization of Marine Mammals made a number of recommendations for studies in the general area of effects of pollution and environmental change on marine mammals (Recommendations 8 and 9, IWC/35/11E).

8.3 Proposals for UNEP

UNEP has officially invited the sub-committee to undertake the development of proposals for the utilisation of funds (US $3 million) to be requested for research on small cetaceans. Guidance from the full Committee was not available in time for consideration of the request at this year's meeting of the sub-committee.

8.4 Advice to FAO concerning unreported incidental catches (see Item 8.5)

8.5 Priority topics for 1984 meeting

Because of an informal request from FAO for information on fisheries taking marine mammals incidentally but for which the mammal take is not presently reported in fishery statistics, and because of concern over the development of several new gillnet fisheries that possibly take small cetaceans, the sub-committee has decided to focus at the 1984 meeting on review of new and expanding fisheries that impact or may impact small-cetacean populations. The group also agreed to review the life histories, population biology and fishery involvement of the species of *Cephalorhynchus: C. hectori, C. heavisidii, C. commersonii* and *C. eutropia*. The sub-committee tentatively agreed to review exploited populations of pilot whales, *Globicephala melaena* and *G. macrorhynchus,* at the 1985 meeting.

8.6 Publication of documents

A list of documents to be considered for publication was submitted to the Editorial Board.

8.7 Review of small-cetacean research proposals

The sub-committee reviewed SC/35/RP8, 11 and 12.

SC/35/RP8 is not a fully developed proposal and its technical aspects cannot be adequately reviewed in its present form. The sub-committee can make two comments, however.

(1) Aerial survey is probably not the best census method for this species; members of the group pointed out that the water in the proposed survey area is often turbid and that the cochito, like the harbour porpoise, almost certainly travels in small groups and spends only a small proportion of the time at the surface (probably less than 10%), making it highly likely that animals would be missed from a plane.

(2) Mexican regulations concerning marine mammal research require that all research projects in Mexico be joint undertakings involving Mexican research entities and scientists. For this reason, the sub-committee recommends that the applicants approach the appropriate Mexican agency and explore the possibility of preparing a joint proposal for submission to the IWC. Perdomo noted that there is interest in Mexico in research on *P. sinus.*

The group feels that SC/35/RP11 should be evaluated by the sub-committee on protected species but support it in principle.

SC/35/RP12 is a revised and expanded version of SC/35/RP5 of last year's meeting. The sub-committee endorsed it then and reiterates the endorsement now, recommending that the proposed 1983 pilot project be funded.

8.8 Errors in IWS

The sub-committee again found extensive errors in the most recent edition of IWS (LXXXIX and XC) (see Appendix 5) and requests the Secretary to write to Mr E. Vangstein regarding these errors.

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Appendix 1

AGENDA

1. Participants, agenda and introductory remarks.
2. Review of documents.
3. Review of exploited populations of phocoenids.
4. Review of populations involved in live-capture fisheries.
5. Review of new data and analyses for Baird's beaked whale, *Berardius bairdii.*
    - 5.1 Refinement and reanalysis of CPUE data.
    - 5.2 Reanalysis of scouting vessel data.
6. Review of new information on Black Sea dolphin populations and fisheries.
7. Review of new information on other exploited small cetaceans.
8. Other business.
    - 8.1 Takes of small cetaceans in 1982 (appendix table).
    - 8.2 New information on the effects of pollution on small cetacean populations.
    - 8.3 Proposals for UNEP.
    - 8.4 Advice to FAO concerning unreported incidental catches.
    - 8.5 Priority topics for 1984 meeting.
    - 8.6 Publication of documents.
    - 8.7 Review of small cetacean research proposals.
    - 8.8 Errors in IWS.

Appendix 2

LIST OF DOCUMENTS

Documents in the SM series are listed on pp. 68–9 of this volume.

Appendix 3

SUMMARY OF AVAILABLE LIVE-CAPTURE INFORMATION

Documented takes of small cetaceans by live-capture fisheries, shown by species and area. Included are animals reported deliberately caught, selected from drive fisheries, or recovered as accidentally entangled/entrapped in fishing gear. Totals do not include animals released on the day of capture.

Footnotes to all Tables

(1) Catches are grouped by broad geographical regions. Such reporting is not meant to imply definitions of populations or stocks.
(2) US records are known to be incomplete. Reliable records have been kept since 1973. Limited data are published or were otherwise available to the sub-committee on known takes prior to 1973.
(3) From SC/35/SM4 Table 6, admittedly only a partial listing. This species has been captured live since about 1861; records should reflect sporadic takes over 121 years.
(4) Reporting period 1973–1982.
(5) From SC/35/SM32 which contains only current holdings for 6 dolphinariums currently operating and does not report previous holdings of these or any captures for at least three other institutions (Cairns, Tweed Heads and Taronga Zoo) (reported by McNamara).
(6) At least 1 individual not reported in SC/35/SM32 was known to have been held at Cairns in the past (reported by Leatherwood).
(7) Includes four released alive within two weeks (SC/35/SM3).
(8) Whereas one is reported to be held in captivity SC/35/SM32, 2 were captured and removed (reported by McNamara).
(9) Dispute exists over exact number of removals (see Bigg and Wolman, 1975; Asper and Cornell, 1977). Includes all captures of *O. orca*, from the Pacific Northwest, as data to separate them were unavailable to the Committee.
(10) Includes 37 exported and two which died in captivity in Iceland.
(11) Includes all recorded captures 1973–1982 and records for one collecting institution 1966–1973 (Walker, 1975). Data were unavailable on other known collections.
(12) Includes one animal noted 'released' but time period not specified (SC/35/SM4).
(13) Reported as *T. aduncus*—different, unresolved total numbers from SC/35/SM2 and SM26, respectively.
(14) Includes 652 listed as *Tursiops truncatus* (1968–1982) and 45 as *T. aduncus* (1973–1982).
(15) Likely an underestimate.
(16) Reporting period 1968–1982.
(17) Includes eight reported as 'escaped' or 'released' but unspecified times after capture and numbers of each.
(18) Includes estimated 1,578–1,615 taken 1914–20 Mar. 1980 (Leatherwood and Reeves, 1982) and about 44 taken in 1980–82 (SC/35/SM4).
(19) Includes 79 animals caught live as fishery by-catch and two intentionally netted (SC/35/SM14, 29)
(20) R-J. Liu, Cambridge University, pers. commn. 1 July 1983.
(21) From Kasuya (1972).
(22) Including 4 (SC/35/SM29) + 3 (SC/35/SM4) + 2 (Pilleri, 1974) + 1 (reported by Brownell).
(23) Does not include takes from Washington (see Note 24).
(24) Includes all animals taken in waters of Washington State and British Columbia, as data to separate them were unavailable to the Committee.

Table 1

Summary table of known live-captures by species and continent.

	The Americas	Asia	Australasia	Africa	Indian Sub-cont.	Europe	Unknown	Total
Ziphius cavirostris	1	—	—	—	—	—	—	1
Monodon monoceros	7	—	—	—	—	—	—	7
Delphinapterus leucas	104–5+	1	—	—	—	—	2	107–8+
Steno bredanensis	17	5	—	—	—	~11	—	~33
Sotalia fluviatilis	45	—	—	—	—	—	—	45
Sousa chinensis	—	2	2+	—	—	—	—	4+
Sousa teuszii	—	—	—	3	—	—	—	3
Orcaella brevirostris	—	16	1	—	—	—	—	17
Peponocephala electra	2–3	12	—	—	—	—	—	14–15
Feresa attenuata	3	—	—	—	—	—	—	3
Pseudorca crassidens	11+	5	2	—	—	—	—	18+
Orcinus orca	58–66	9	—	—	—	39	1	107–115
Globicephala macrorhynchus	70	156	—	—	—	—	—	226
Lagenorhynchus albirostris	5	—	—	—	—	—	—	5
Lagenorhynchus obscurus	—	—	22–24	23	—	—	—	45–47
Lagenorhynchus obliquidens	79	238	—	—	—	—	—	317
Lagenodelphis hosei	—	16	—	—	—	—	—	16
Tursiops truncatus	1,732–69+	773–87	32+	23	—	6	64	2,630–81+
Grampus griseus	1	50	—	—	—	1	—	52
Stenella longirostris	85+	10	—	—	—	—	—	95+
Stenella attenuata	62+	69	—	—	—	—	—	131+
Delphinus delphis	37+	1	28	—	—	24	—	90+
Lissodelphis borealis	9	—	—	—	—	—	—	9
Cephalorhynchus hectori	—	—	4	—	—	—	—	4
Cephalorhynchus commersonii	24	—	—	—	—	—	—	24
Phocoena phocoena	occasional	1	—	—	—	81+	—	82+
Phocoenoides dalli	8+	8+	—	—	—	—	—	16+
Neophocaena phocaenoides	—	107	—	—	—	—	—	107
Platanista gangetica	—	—	—	—	7	—	—	7
Platanista minor	—	—	—	—	10	—	—	10
Inia geoffrensis	100+	—	—	—	—	—	—	100+
Total	2,460–2,507+	1,479–1,493+	91–94+	49	17	162+	67	4,325–4,387+

Table 2

Summary table of live-captures in the Americas.

	United States[2]					Canada		Central and S. America			
	Hawaii	Alaska	NE coast	Southeast	Pacific	West coast	E and NE coast	Mexico	North east	Argentina	Total
Z. cavirostris	—	—	—	—	1	—	—	—	—	—	1
M. monoceros	—	—	—	—	—	—	7	—	—	—	7
D. leucas	—	10+	—	—	—	—	94–95[3]	—	—	—	104–5+
S. bredanensis	17	—	—	—	—	—	—	—	—	—	17
S. fluviatilis	—	—	—	—	—	—	—	—	45	—	45
P. electra	2–3	—	—	—	—	—	—	—	—	—	2–3
F. attenuata	3	—	—	—	—	—	—	—	—	—	3
P. crassidens	10+	—	—	—	1	—	—	—	—	—	11+
O. orca	—	—	—	—	—	58–66[9]	—	—	—	—	58–66
G. macrorhynchus	20	—	—	—	50[11]	—	—	—	—	—	70
L. albirostris	—	—	—	—	—	—	5	—	—	—	5
L. obliquidens	—	—	—	—	79[11]	—	—	—	—	—	79
T. truncatus	34[12]	—	?	1,622–59[18]	18+[11]	—	—	58	—	—	1,732–69+
G. griseus	—	—	—	—	1	—	—	—	—	—	1
S. longirostris	85+[17]	—	—	—	—	—	—	—	—	—	85+
S. attenuata	47	—	—	15+	—	—	—	—	—	—	62+
D. delphis	—	—	—	?	37+[11]	—	—	—	—	—	37+
L. borealis	—	—	—	—	9[11]	—	—	—	—	—	9
C. commersonii	—	—	—	—	—	—	—	—	—	—24	24
P. phocoena	—	←— occasional —→			—	occasional	—	—	—	—	occasional
P. dalli	—	—	—	—	8+[11]	—	—	—	—	—	8+
T. geoffrensis	—	—	—	—		—	—	—	100+	—	100+
Totals	218–19+	10+	?	1,637–74+	204+[23]	58–66[24]	106–7+	58	145+	24	2,460–507+

Table 3

Summary table of live-captures in Asia (excluding the Indian sub-continent).

	Indonesia							
	Java	Borneo	Philippines	Japan	Taiwan	Hong Kong	People's Republic of China	Total
D. leucas	—	—	—	1[4]	—	—	—	1
S. bredanensis	—	—	—	5[4]	—	—	—	5
S. chinensis	—	—	—	—	—	2	—	2
O. brevirostris	—	16	—	—	—	—	—	16
P. electra	—	—	10[7]	2[4]	—	—	—	12
P. crassidens	—	—	—	5[4]	—	—	—	5
O. orca	—	—	—	9[4]	—	—	—	9
G. macrorhynchus	—	—	—	156[4]	—	—	—	156
L. obliquidens	—	—	—	238[4]	—	—	—	238
L. hosei	—	—	16	—	—	—	—	16
T. truncatus	16	14–28[13]	—	697[14]	45	1	—	773–87
G. griseus	—	—	—	50[16]	—	—	—	50
S. longirostris	9	—	1	—	—	—	—	10
S. attenuata	—	—	—	69[4]	—	—	—	69
D. delphis	—	—	—	1[19]	—	—	—	1
P. phocoena	—	—	—	1[4]	—	—	—	1
P. dalli	—	—	—	8+[4]	—	—	—	8+
N. phocaenoides	2	—	—	94[19]	—	—	11+[20]	107+
Totals	27	30–44	27	1,336+	45	3	11+	1,479–93+

Table 4

Summary table of live-captures in Europe.

	Mediterranean Sea	Adriatic Sea	Western Europe	Denmark	Iceland	Total
S. bredanensis	~10	—	1	—	—	11
O. orca	—	—	—	—	39[10]	39
T. truncatus	2	2	2	—	—	6
G. griseus	1	—	—	—	—	1
D. delphis	22	—	2	—	—	24
P. phocoena	—	—	—	81+	—	81+
Total	~35	2	5	81+	39	162+

Table 5

Summary table of live-captures for the rest of the world.

	India and Bangladesh	Pakistan	South Africa	New Zealand	Australia	Total
S. chinensis	—	—	—	—	2+[5]	2+
S. teuszii	—	—	3	—	—	3
O. brevirostris	—	—	—	—	1[6,5]	1
P. crassidens	—	—	—	—	2[8,5]	2
L. obscurus	—	—	23	22–24	—	45–7
T. truncatus	—	—	23	4	28+[5]	55+
D. delphis	—	—	—	28	—	28
C. hectori	—	—	—	4	—	4
P. gangetica	7[21]	—	—	—	—	7
P. minor	—	10[22]	—	—	—	10
Total	7	10	49	58–60	33+	157–9+

Appendix 4

REPORTED CATCHES OF SMALL CETACEANS IN 1982

Species		Canada	Denmark	France	Japan	Iceland	Non-US ETP	Turkey	USA	Other	Total
Baird's beaked whale, *Berardius bairdii*	D	—	—	—	60^{J}	—	—	—	—	—	60
Cuvier's beaked whale, *Ziphius cavirostris*	D	—	—	—	—	—	—	—	—	x^{15}	x
Narwhal, *Monodon monoceros*	D	402^{C}	$342–400^{G}$	—	—	—	—	—	—	—	> 744
White whale, *Delphinapterus leucas*	D	475^{C}	$225–400^{G}$	—	—	—	—	—	$298–354^{9}$	139^{16}	> 1,137
False killer whale, *Pseudorca crassidens*	D	—	—	—	1^{J}	—	—	—	—	—	1
Killer whale, *Orcinus orca*	D	—	—	—	4^{J}	—	—	—	—	3^{K}	7
	I	—	—	—	1^{J+3}	1^{I}	—	—	—	—	2
	L	—	—	—	—	5^{I}	—	—	—	—	5
Long-finned pilot whale, *Globicephala melaena*	D	—	2,652F	—	—	—	—	—	—	—	2,652
	L	—	—	$> 1^{2}$	—	—	—	—	—	x^{15}	> 1
Short-finned pilot whale, *G. macrorhynchus*	D	—	—	—	395^{J}	—	—	—	—	—	395
	I	—	—	—	3^{J}	—	—	—	x^{10}		> 3
	L	—	—	—	6^{3}	—	—	—	2^{11}		8
Pacific white-sided dolphin, *Lagenorhyncus obliquidens*	D	—	—	—	171^{J+4}	—	—	—	—	—	171
	I	—	—	—	4^{J}	—	—	—	—	—	4
	L	—	—	—	13^{3}	—	—	—	2^{11}		15
Fraser's dolphin, *Lagenodelphis hosei*	D	—	—	—	—	—	—	—	—	x^{3}	x
Bottlenose dolphin, *Tursiops truncatus*	D	—	—	$> 1^{2}$	831^{J}	—	—	x^{8}	—	$7^{3} + x^{15}$	> 839
	I	—	—	—	3^{J}	—	—	—	—	x^{17}	> 3
	L	—	—	—	61^{3}	—	4^{6}	—	23^{11}	—	88
Risso's dolphin, *Grampus griseus*	D	—	—	—	4^{J}	—	—	—	—	x^{15}	> 4
	I	—	—	—	2^{J}	—	—	—	—	x^{15}	> 2
Spotted dolphin, *Stenella attenuata*	D	—	—	—	$3,799^{J}$	—	—	—	—	—	> 3,799
	I	—	—	—	—	—	$3,189–3,847^{7}$	—	15,590–19,058	—	> 18,779
Spinner dolphin, *S. longirostris*	I	—	—	—	—	—	$705–850^{7}$	—	$5,972–7,301^{7}$	—	> 6,677
Striped dolphin, *S. coeruleoalba*	D	—	—	$> 2^{2}$	$2,016^{J+4}$	—	—	—	—	x^{15}	> 2,018
	I	—	—	$> 1^{2}$	25^{J}	—	$97–117^{7}$	—	$471–575^{7}$	x^{17}	> 594
Common dolphin, *Delphinus delphis*	D	—	—	$> 3^{2}$	99^{J+4}	—	—	x^{8}	—	x^{15}	> 102
	I	—	—	$> 5^{2}$	102^{J}	—	$88–106^{7}$	—	$414–506^{7}$	x^{17}	> 609
Northern right whale dolphin, *Lissodelphis borealis*	D	—	—	—	3^{4}	—	—	—	—	—	3

[continued]

Species		Canada	Denmark	France	Japan	Iceland	Non-US ETP	Turkey	USA	Other	Total
Commerson's dolphin, *Cephalorhyncus commersonii*	D	—	—	11^{2}	—	—	—	—	—	—	11
Harbour porpoise, *Phocoena phocoena*	D	—	554–700^{G}	—	57^{J}	—	—	x^{8}	—	—	> 611
	I	> 317^{1}	—	~10^{1}	66^{J}	63^{1}	—	—	55–> 200 {US + 1 + 13 + 12	x^{1}	> 511
	L	—	—	—	—	—	—	—		1^{6}	1
Dall's porpoise, *Phocoenoides dalli*	D	—	—	—	12,833^{J}	—	—	—	—	—	12,833
	I	—	—	—	4,916–12,132^{5}	—		—	x^{14}	—	> 4,961
Finless porpoise, *Neophocaena phocaenoides*	I	—	—	—	5^{3}	—	—	—	—	x^{18}	> 5
	L	—	—	—	10^{3}	—	—	—	—	—	10
Unidentified or mixed		—	—	> 1^{2}	30^{J}	—	—	—			> 31
		—	—	—	91^{J}	—	132–159^{7}	—	617–754^{7}	{1,473–3,237^{19} 15,100^{20}	> 17,183
Total		> 1,194	> 3,773	> 35	> 25,656	69	> 4,215	x	> 23,444	> 16,493	> 74,879

Key, sources and notes. D = direct take; I = incidental capture; L = live capture; x = known to have occurred but no data available; C = Progress Report Canada; G = Greenland; F = Faroe Islands; J = Japan. I = Iceland; US = USA; K = Republic of Korea; 1 = SC/35/SM24, estimated catch; 2 = Collet; other catches are known to occur but there is no new information. 11 Commerson's dolphins were taken for scientific studies.; 3 = SC/35/SM26, with comments by Leatherwood on occasional takes of Fraser's dolphin in Taiwan; 4 = SC/35/SM10; 5 = The first number is the take reported in SC/35/SM28 and ProgRep Japan. The second number is a US estimate for take in the salmon gillnet fishery (SC/35/SM8); 6 = SC/35/SM29; 7 = SC/35/SM16, estimated catch; 8 = E. Akyuz, FAO Rome, *in litt.* to S. J. Holt; 9 = White whales captured by Alaskan Eskimos, data provided by Alaska Department of Fish and Game (for known catches), and estimated takes by Braham.; 10 = Perrin; 11 = SC/35/SM4, incomplete data for bottlenose dolphin; 12 = SC/35/SM5; 13 = D. G. Ainley and S. Allen; 14 = Balcomb; 15 = Duguy *et al.*, 1982. Known to occur off Spain, France and Italy; 16 = Catch outside the Antarctic in 1982, white whales taken by USSR; 17 = A. Aguilar; 18 = SC/35/SM2, occasional takes known in Java; 19 = SC/35/SM21, estimated incidental catches by Taiwanese vessels in Australian waters, including *T. truncatus* + *S. longirostris* + *S. attenuata* + *P. crassidens*, incomplete data as there is no information on catches in shark nets and live-capture fisheries for 1982; 20 = Estimate of catches in 1982 for Sri Lanka, including *S. longirostris* + *S. bredanensis* + *T. truncatus* + *Z. cavirostris* + *Mesoplodon sp.*—Alling, 1983 in SC/35/SM6.

Appendix 5

ERRORS IN SPECIES LISTINGS IN INTERNATIONAL WHALING STATISTICS LXXXIX AND XC

(1) In Tables Z^2 (p. 28–32) and Z^{10} (p. 42), the data for harbour porpoise, *Phocoena phocoena*, and common dolphin, *Delphinus delphis*, have been confounded. The catches by Denmark listed under 'common porpoise' were of *P. phocoena*. The catches by the US also listed under 'common porpoise' were actually of *D. delphis*.

(2) The USSR catches of southern bottlenosed whales (data from Table Z^4, p. 36) are incorrectly called *Hyperoodon ampullatus*. If all these whales were in fact all *Hyperoodon*, they would be *H. planifrons*.

(3) It was also noted that Table Z^5 (p. 37) referred to catches of pilot whales around Japan and British West Indies as *Globicephala melaena*. All of these pilot whales were *G. macrorhynchus*.

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Report of the Workshop

Edited by
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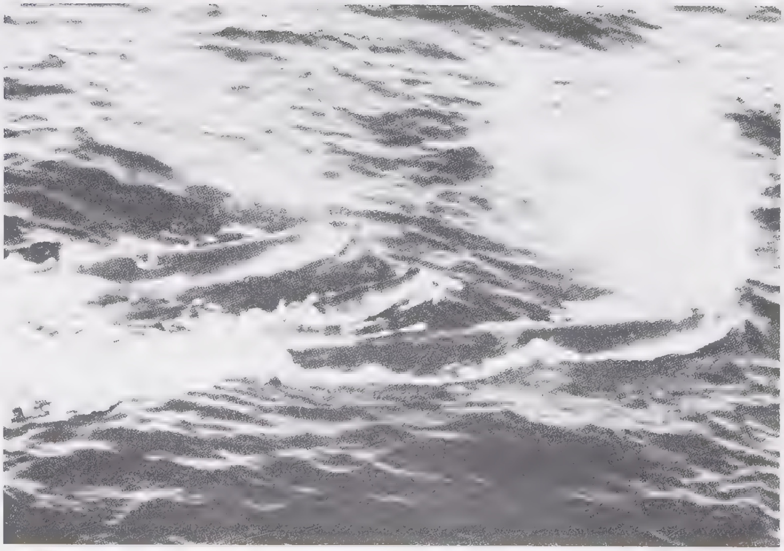

Sperm Whales

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I. INTRODUCTION

The main charges to the workshop were to examine the interpretation of ovarian corpora, to review the reproductive components of quantitative models currently used in assessment and management, and to explore how research in the field and laboratory on the one hand and quantitative modelling on the other, can be better integrated. The agenda (Appendix A) was structured to alternate group discussions and laboratory sessions. Discussion leaders and rapporteurs prepared draft reports that formed the basis for this report. The organization and content of the report do not correspond entirely to the workshop agenda, but rather reflect the course of the discussions. Participants in the workshop are indicated in the list of conference participants at the beginning of this volume.

The following participants acted as discussion leaders and/or rapporteurs during the workshop sessions: Barlow, Benirschke, Braham, Brownell, DeMaster, Donovan, Goodman, Hester, Kirkwood, Lockyer, Marsh, Mead, Mizroch, Odell, Perrin, Reilly and Wells. Marsh and Benirschke prepared the meeting draft and subsequent revisions of Appendix B.

II. QUESTIONS OF MORPHOLOGY AND PHYSIOLOGY

(A) Interpreting ovarian scars

Implicit in the use of ovulation rate as a vital parameter in modelling reproduction of cetaceans (see Section B) is the assumption that corpora albicantia (CA) persist through life and thus reflect the actual number of ovulation events. Some workers have also assumed that corpora of simple ovulation can be distinguished from those of pregnancy, yielding an accurate history of calf-bearing.

(1) *Do corpora albicantia persist indefinitely?*

The consensus opinion is that CAs do persist indefinitely in the ovaries of at least some cetaceans, e.g. sei whales and fin whales (Gambell, 1968; Laws, 1961). It is likely, however, that not every ovulation results in a corpus luteum (CL). This can be investigated only by steroid monitoring coupled with ovarian histology. The implication of this possibility is that we cannot necessarily assume that ovulation rate is measurable by counting corpora.

For the short-finned pilot whale, *Globicephala macrorhynchus*, no major gaps in the size distribution of CAs indicative of CA disappearance were noted and they are thought to persist indefinitely (Marsh and Kasuya, this volume). The smallest were about 3 mm in diameter. Ohsumi reported that the same is true for the sperm whale, *Physeter macrocephalus*, although final size is greater (about 8 mm in diameter, Gambell, 1972). CAs may also persist indefinitely in *Stenella* spp. (Perrin and Reilly, this volume); however, it was noted that some apparently 'old' females have shrunken ovaries with relatively few CAs. Two explanations were suggested: as a result of ovarian shrinkage many CAs were still present but no longer detectable by gross observation; or some types of CAs may disappear while others persist. The group recommends that the shrunken ovaries be re-examined, using histological techniques, to determine if very small CAs have been missed.

Regarding rate of CA regression, data from *Globicephala* spp., *Stenella* spp., *Delphinus delphis* and other species indicate that CLs regress very quickly initially (first few days or weeks), then slowly thereafter. Regression in the sei whale is rapid immediately after calving, from about 84 mm to about 36 mm in diameter in the first month, then slowing during the balance of the lactation period. Minimal size is reached after perhaps years or decades (Gambell, 1968).

A distinction has been made in some studies between corpora atretica and CAs. In *G. macrorhynchus*, for example, the size distribution of corpora atretica is very different to that of CAs. Corpora atretica shrink to a smaller size (< 1 mm) and may ultimately disappear (Marsh and Kasuya, this volume). Kasuya, Miyazaki and Dawbin (1974) were able to distinguish these two types of corpora for *Stenella* spp. in the western Pacific, but this is not true for the eastern Pacific populations of the same species (Perrin, Coe and Zweifel, 1976). Consequently, corpora counts and size distributions for these two areas for similar species may not be strictly comparable.

Marsh noted much variation in the number of corpora atretica in mature *G. macrorhynchus*, ranging from 0 to 34 per pair of ovaries (usually less than ten). Some of the whales with very high numbers of corpora atretica were found to have low CA counts for their age, but not all with high corpus atreticum counts had low CA counts.

(2) *Are corpora albicantia of simple ovulation distinguishable from those of pregnancy?*

The group concluded that a difference cannot be discerned with currently used methods. Marsh, Ohsumi and Benirschke reported no discernable difference for odontocetes, either macroscopically or histologically. It has been reported by Laws (1961) that no difference exists for fin whales. However, Zimushko (1970) reported that he could distinguish the two types of CAs in gray whales. Other Soviet researchers report similar findings (Ivashin, this volume). Ivashin mentioned his (1958) study in which this was also done for humpback whales, based on the size of the CA, under the assumption that a CL of pregnancy regresses more slowly than a CL of ovulation only. He also reported finding morphological differences between CLs of pregnancy and of ovulation. It was pointed out, however, that lactation can affect the rate of regression, and it was agreed that size of the CA alone, (even when adjusted for age) cannot be considered an indicator of the original nature of the event giving rise to it. Marsh noted that in *G. macrorhynchus* large CAs do not appear to regress further during pregnancy and suggested that in this species the rate of regression of a CA may be affected by hormonal status. In contrast, Larsen reported that he found significant regression of corpora during pregnancy in minke whales.

The group discussed possible new techniques to distinguish between CLs of pregnancy and ovulation. Erickson noted that the compound relaxin appears in a CL of pregnancy but not in a CL of ovulation, and it is only necessary to freeze specimens very soon after death to test tissues for presence of this substance. The substance disappears rapidly during regression of the CL. However, it is necessary to fix ovaries properly and immediately following death in order to examine structure at this level, and this may be impractical under field conditions. Miyazaki suggested that since organochlorines (PCBs and DDT) are flushed from a female during lactation (Tanabe, Tanaka and Tatsukawa, 1981), perhaps differential presence of these residues may be used to distinguish between CLs of the two types; work on this is in progress in Japan. Ohsumi noted that it should be possible to determine whether a female with one CA has been pregnant by histological examination of the mammary glands. This may offer a method of identifying reference CAs of the two types so that they can be compared histologically.

(B) Variation in ovulation rate

(1) *Variation among species*

It is clear that there is great variability among species. Evidence for varying ovulation rates exists in the literature for both mysticetes and odontocetes. For example, in Southern Hemisphere fin whales, the ovulation rate is one corpus per 1.4 years (Lockyer, 1972; Gambell, 1973) whereas in minke whales the rate is approximately one corpus per year (Masaki, 1979). For the sperm whale, Gambell (1973) has calculated a mean ovulation rate of 1 corpus per 2.33 years. For the gray whale, a rate of one ovulation per 1.93 years has been calculated (Reilly, this volume).[1]

(2) *Variation within species*[2]

Mizroch (1981) has found evidence of age-specific ovulation in southern fin whales, the rate decreasing in old animals. Evidence by Best (1967; 1980) and Gambell (1972) for sperm whales and Marsh and Kasuya (this volume) for pilot whales suggests a fall-off in rate with older age. Sergeant (1962) reported that in *G. melaena* there is evidence of multiple ovulations per pregnancy in young females. Similar findings have been reported for *Lagenorhynchus obliquidens* (Harrison, Brownell and Boice, 1972).

There are indications that frequency of ovulation as recorded in CAs (disregarding the question as to whether every ovulation results in a CA) decreases in older individuals in some populations, while *per-capita* pregnancy rate does not. This was reported by Mizroch for Southern Hemisphere fin whales (although other factors, such as the difficulty of accurate age determination, may be involved) and by Kasuya for western Pacific striped dolphins, *Stenella coeruleoalba*. The implication is that decline in frequency of CAs with age does not necessarily indicate a decline in pregnancy rate.

Gambell (1968; 1972) has used regression rates of corpus size to estimate age-independent ovulation rates from sei and sperm whales in catches. Lockyer, Gambell and Brown (1977) also used this technique to determine ovulation rates for fin whales taken in the Icelandic catch. However, Collet and Harrison (1981) found that in *Delphinus delphis* the rate of regression of a corpus is not constant but seems to follow a complex pattern. Perrin reported data from *Stenella longirostris* in the eastern Pacific for two stocks, one heavily exploited and the other lightly exploited (Perrin and Henderson, this volume). His data on size frequency of CAs indicate that young females in the more-exploited stock have a lower number of ovulations per unit of age.

Recent studies of reproductive physiology have determined that captive dolphins may have highly variable ovulation rates. Kirby and Ridgway (this volume) reported multiple ovulations per year for *Tursiops* and *Delphinus*, and Wells (this volume) reported similar findings for *Stenella*. Kirby also found that a female that is anoestrous one year may cycle the next. Based on ovarian morphology, Collet and Harrison (1981) observed multiple successive ovulations in *D. delphis* and possible variation in ovulation rate related to age and social hierarchy.

Benirschke noted that similar variation in ovulation rates occurs in other mammals. Some human females ovulate only once per year. There is also evidence in the literature of 'sterile ovulations', or Graafian follicles without eggs in humans. It can be assumed that these become corpora atretica. Mules also exhibit sterile ovulations in which a CL-like body forms and the follicle becomes atretic.

(3) *Accessory corpora lutea*

Accessory CLs, defined as occurring when there is more than one CL per foetus in a pair of ovaries, are found in some species. After a brief discussion on the differentiation between the main CL and the accessory corpora, a consensus was reached that in most cases one cannot differentiate between the two, and further that one cannot distinguish between a CA formed from the regression of an accessory CL and one formed from the regression of a primary or single CL. This led to the question of the interpretation of ovulation rates in species that are known to have accessory corpora. It was agreed that for species in which accessory corpora are likely to occur and the rate of occurrence is known, the estimated ovulation rate should be adjusted, as, for example had been done for *Delphinapterus leucas* by Sergeant (1973).

The group agreed that nothing is known of the origin or function of accessory CLs. They seem to be most common in the odontocete genera *Delphinapterus* and *Monodon*, where they have been reported as occurring in about 12% of pregnant females (Brodie, 1972; K. Hay, pers. comm.). Members of the group reported them as being very rare in all *Balaenoptera* species, *Megaptera*, *Eschrichtius*, *G. macrorhynchus*, *Delphinus delphis*, *Stenella longirostris*, *S. attenuata* and *S. coeruleoalba*. Mitchell reported an occurrence of 0.45% in fin whales taken in the former hunt in the maritime provinces of Canada. Laws (1961) reported a rate of 3.5% and Gambell (1968) a rate of 2.0% in fin and sei whales respectively in the Southern Ocean.

(C) Biases in estimating the reproductive interval

It was noted that calf mortality may shorten the average reproductive interval of a female if that female is capable of becoming pregnant shortly after a calf's death. Several factors were identified that might influence the time between calf loss and re-impregnation: (i) the age of the calf at death; (ii) the degree and timing of reproductive seasonality; (iii) Kirby & Ridgway (this volume) presented evidence that *Tursiops* females in captivity tend to ovulate seasonally and need not be synchronous within a group. This may also influence the length of time between calf death and the next ovulation.

Calf death would, in effect, shorten the average lactation time in a population. Depending on how the reproductive interval is estimated, calf death can introduce a bias. For instance, 'method 2' of Perrin *et al.* (1976), which is based on the maximum length of calves assumed to accompany lactating females, estimates reproductive interval from something that is closer to the maximum lactation time rather than the average. Calf death would thus increase the bias that is inherent in this method. However, 'method 1' in the same paper, which is based only on proportion of adult females lactating, would not be biased in its estimate of reproductive interval by calf death. It should be remembered when using this method that the calving intervals calculated are averages that include some cycles for which fetal or neonatal death may have decreased the time to re-impregnation.

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[1] Editors' note. Other published ovulation rates (years per corpus) include: Bryde's whales – Best (1977), 0.4 (S. African inshore), 2.4 (offshore); sei whales – Lockyer and Martin (1983) 1.7 (N. Atlantic), Gambell (1968) 1.4 (S. Hemisphere); fin whales – Lockyer and Brown (1979) 1.6 (N. Atlantic); minke whales – Kato (1982) 1.1–1.2 (S. Hemisphere); humpback whales – Chittleborough (1965) 0.9 (S. Hemisphere); sperm whales – Best (1974) 1.7–3.0 (review of various estimates).

[2] Editors' note. Best (1977) reported an interesting variation in ovulation rates for Bryde's whales found in Southern African waters: the average number of ovulations per reproductive cycle was found to be 3.75 for whales of the 'inshore' form but only 1.00 for whales of the 'offshore' form.

(D) Definition of 'sexual maturity'

The group discussed the question of whether the usual definition of the attainment of sexual maturity in females as being the first ovulation is adequate for modelling purposes. Pubescent females may ovulate more than once before conceiving. It was concluded that three criteria of maturity are useful: first ovulation, first conception and first lactation. The first can be ascertained from examination of ovaries. With regard to ascertaining conception, Benirschke noted that the gross aspect of the uterus in terms of development of stretch marks along the uterine body, marked increase in diameter of the uterine horns and the increase in vascular supply to the uterus, are all indications that the female has borne a large foetus. In addition, the myometrium may show changes in its histology in terms of thickening and vascularity which persist after a pregnancy. These all indicate that the female has born a foetus of substantial size but will occur regardless of whether the foetus is aborted or borne until term. Benirschke also reported that there are irreversible changes in the mammary gland that reflect lactation. These indicate whether a female has borne her calf until at least full term but not whether she has successfully maintained it until weaning.

Histological examination of the endometrium from both cornua may be helpful in identifying whether or not pregnancy existed at the time of capture in situations which are known to have a high risk of causing foetus loss, either through mode of operation of a fishery resulting in spontaneous abortion and/or during work-up of the carcass.[3]

It was noted that in newly-mature fin and sei whales, the apparent pregnancy rate is similar to that for older ages (Laws, 1961; Gambell, 1968) and hence in these and other baleen whales, age at first ovulation is perhaps still the best definition of age at attainment of sexual maturity.

(E) Male seasonality

The group discussed the question of seasonal aspermatogenesis in cetaceans. Several examples were noted of reduced activity evidenced by decrease in testis weight, but histological evidence for aspermatogenesis was cited for only 3 odontocetes: *Delphinus delphis* (Collet and St. Girons, this volume), *Phocoenoides dalli* (by Kasuya) and *Monodon monoceros* (K. Hay, pers. comm.), and two mysticetes: fin whales (Laws, 1961) and humpback whales (Chittleborough, 1955). Gambell (1968) did not find histological evidence of seasonality in *B. borealis*. Collet reported that while she found aspermatogenesis in most adult males in the eastern north Atlantic population of *D. delphis*, during the apparent breeding season (February to November), at least some individuals were spermatogenic throughout that period. This suggests that in this area, while there is an overall pattern of seasonality in breeding, male seasonality may be individual rather than populational. Some of the participants were of the opinion that the activity of a single male should not make any difference as long as there are enough sexually active males to service all of the sexually active females, but some other participants thought that the seemingly complex social structure in odontocetes could make the status of individual males more important, e.g. as in the polygynous mating system of sperm whales.

Kasuya noted that in *G. macrorhynchus* in Japan, the pubertal animals produce small amounts of sperm in the breeding season but no sperm in the nonbreeding season.

Perrin described seasonal change in testes weight in two populations of *Stenella longirostris* in the eastern tropical Pacific with different histories of exploitation by the tuna purse-seine fishery (Perrin and Henderson, this volume). Males that have combined testis-epididymis weight of more than 700 g are fully 'potent', that is, have copious sperm in the epididymes. In the less exploited population (northern whitebelly spinners) a large proportion (about 50%) of adult males attain such testis weights seasonally (in February and in July–August), with maximum weights of more than 2 kg. In the more exploited population (eastern spinners), testis weights increase seasonally, but only a very small number of adult males (less than 5%) reach testis weights of 700 g or more, and maximum recorded testis/epididymis weight is less than one kg. This is correlated with lower pregnancy rates in young, but not old, females in this population. It is possible that some aspect of the exploitation has resulted in reproductive difficulties in the more heavily exploited population. The group agreed that this phenomenon should have high priority for further investigation, as it runs counter to the conventional wisdom that lower density (due to exploitation) leads to higher reproductive rates.

It was agreed that from the point of view of assessing male sexual maturity, in addition to recording testis weights, both the routine examination of the epididymis for sperm and the histological examination of smears of the testis tissue from the periphery and centre are essential to differentiate between immature, pubertal, active and resting mature animals. This is especially important because of the fact that an inactive older male can have testes larger than those of a younger but active male (as found for *D. delphis* by Collet and St. Girons, this volume).

Indications of seasonal testicular activity for dolphins are also available from studies of reproductive physiology. Wells (this volume) found an apparent annual cycle in testosterone production in male *Stenella longirostris*, and Kirby and Ridgway (this volume) reported seasonal variation in testosterone concentrations for *Tursiops*.

(F) Pathology and Anomalies

(1) *Reproductive senescence*

Senescent ovaries apparently exist in some odontocete cetaceans, but they have not been found in mysticetes. Marsh reported that in *G. macrorhynchus* from Japan, such ovaries are characterized macroscopically by a lack of follicles, CLs and young or partially regressed CAs. Histological samples indicate a lack of primordial and Graafian follicles, with much of the tissue being fibrotic and sclerotic. While there is no evidence of follicular activity, numerous, generally easily counted CAs may be evident both macroscopically and microscopically. In the 50-year-old pilot whale presented in the laboratory session as an example, there were 13 CAs present. Sergeant (1962) reported up to 14 corpora in ovaries of apparently senescent *G. melaena* females.

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[3] Editors' note. E.g. see Martin (1982).

Female *G. macrorhyncus* exhibit a high incidence of reproductive senescence. Marsh and Kasuya (this volume) found that although females live up to about 63 years, the oldest pregnant female was 34.5 years, the oldest with a CL of ovulation was 37.5 years; and the oldest with a young CA was 38.5 years. Sixty-one (26%) of the 235 mature females sampled were older than 35 years, and ten of these, including the 50-year-old example given above, were lactating. The old lactating females did not show any greater ovarian activity than other old females.

Perrin reported that reproductive senescence in *Stenella* spp. is probably indicated by the presence of 'withered' ovaries (Perrin *et al.*, 1976; Perrin, Holts and Miller, 1977). This condition first appears when there are ten or more corpora present in the ovaries. The frequency of 'withered' ovaries in *Stenella* appears to be very low, on the order of 0.1%, but this figure should be considered approximate as it is not known if these females may be more vulnerable to capture. A comparison of the *Globicephala* spp. with the *Stenella* spp. suggests that the frequency of reproductive sensescence may be quite variable from species to species within the odontocetes.

Changes in ovulation rates (discussed above) may be indications of reproductive senescence, but the available evidence is inconclusive.

Reproductive senescence has not been reported for baleen whales. Withered ovaries have not been found, nor have any whales lacking follicular activity been seen in several hundred ovaries examined by Lockyer and colleagues. Female whales over 70 years old have been examined and still exhibit folliculate activity; as many as 50 corpora have been found in some ovaries (although no accessory CLs have been reported).

In summary, reproductive senescence apparently exists in some cetaceans, although it has not yet been identified for baleen whales, and may be of a highly variable frequency from species to species in the odontocetes. The question remains of why it should exist at all; the answer probably cannot be obtained except through sociobiological research.[4]

(2) *Cystic follicles and ovarian cysts*

Cystic follicles can apparently only be distinguished from mature follicles on the basis of histology. During a given ovarian cycle, follicle stimulating hormone (FSH) induces many follicles to develop, and the granulosa cells begin to multiply. When an egg is released from one follicle and pregnancy occurs, the others become atretic i.e. cystic with some thecal luteinisation. During atresia, the granulosa cells are the first to die. The loss of or change in the granulosa cells provides the distinction between cystic follicles and mature follicles, but the distinction cannot be made grossly. The group recommends that identification of such bodies be made through histological examination. Information on occurrence and histology of cystic follicles and other 'ovarian cysts' in baleen whales is contained in Laws (1961) and Gambell (1968).

(3) *Parasites*

In dolphins, parasites are frequently found in the lungs or in the hilus of the reproductive tract but generally are not on the surfaces where they can interfere with reproduction. Tapeworm cysts (*Monorygma* sp.) have been seen in the ovarian hilus of *Stenella* spp., forming flimsy adhesions to the ovarian surface. Usually there is fibrosis around the cysts, and histologically some granuloma formation; the granuloma are an indication of the animal's mobilization against the foreign organism. It is believed that these parasites do not interfere with the reproductive function of the ovary.

Parasites have been found to lower reproductive success in at least two cases, however. Geraci, Dailey and St. Aubin (1978) found that parasites in the mammary glands can interfere with successful calf-rearing in *Lagenorhynchus acutus* (through necrosis of mammary tissue), and Walker reported a similar situation in *Phocoenoides dalli*. The rate of infection and its consequences as reported for *L. acutus* suggest that parasitism can significantly affect reproduction in a population.

(4) *Abortion*

Abortions occur in cetaceans, but determining if an abortion has occurred when there is no foetus in the vagina is difficult. In the absence of an obvious foetus, neither macroscopic nor histologic examination can confirm abortion, but certain criteria can be used to provide the impetus to look more closely for a possible aborted foetus. The presence of a recent CA, asymmetry of the uterine horns and histologic differences between the horns suggest abortions. Differences in the uteri include a thickened endometrium with evidence of chronic inflammation and remnants of secretions and placental tissue in the larger horn. Abortions of pre-implantation embryos will show only minimal changes in the uterus, and will therefore be even more difficult to detect.

Ichihara (1962) reported on 13 incidences of prenatal death of the foetus in fin whales taken in the Antarctic. The great majority of these incidences occurred in older mothers with 10 or more corpora. Ichihara estimated a minimal prenatal death rate of 0.14% for animals actually observed. Prenatal death in early pregnancy had resulted in rapid foetal disintegration and reabsorption whilst that in late pregnancy resulted in mummification and retention for long periods; lack of a CL and partial decomposition of the foetus had commenced. Prenatal death was observed most frequently for multizygotic foetuses yet one dead and one live foetus were discovered simultaneously in one uterus. A few of the foetuses were deformed.

(5) *Multiplets*

Multiplets have been found *in utero* in cetaceans, but there is no evidence of mature delivery of these young. About 1% of fin whale foetuses are twins (Laws, 1961; Gambell, 1968) and Mizroch reported that this proportion had not changed from 1931–1974. About 25 of 95,000 (0.003%) pregnant fin whales reported to the International Bureau of Whaling Statistics had triplets in their uteri. Jonsgård (1953) reported a fin whale with 6 foetuses, of varying sizes. All of these multiple foetuses have been smaller than term. Kimura (1957) reported multiplet frequencies of 0.57% for humpback whales to 2.28% for sei whales. Kato (1982) reported 0.56% twins and 0.03% triplets for Southern Hemisphere minke whales. The largest fin whale twin was reported to be about 20 ft long, but most were 12 ft or less in length. Two sets of sei whale twins, including one conjoined pair, were about 6 ft long. Multiple calves accompanying their presumed mothers have not been seen in long-term field observations of *Tursiops* or *Stenella* populations by Scott or Wells, nor have they been reported for baleen whales except for a drawing of a humpback whale with two calves published by Scammon (1874).

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[4] Editors' note. There will be some discussion of this in *Rep. int. Whal. Commn* (special issue 8): Behaviour of Whales in Relation to Management, which will be published in late 1984 or early 1985.

Benirschke noted that the frequency of *in utero* twins for fin whales is similar to that reported for humans. Humans have an average twinning frequency of 1–2%, but this is highly variable between races. For example, some African tribes have a frequency of 5%, while in Japan the rate may be 0.5 to 0.7%.

The rate of twinning may increase with age in cetaceans, e.g. 0.1% (at 1–5 corpora) to 6.25% (at 30–35 corpora) in Southern Hemisphere fin whales, (Kimura, 1957).

Both monozygotic and dizygotic twins have been reported for the Cetacea. The presence of conjoined or incompletely-split foetuses indicates the existence of monozygotic or identical twins. The presence of two foetuses with a single CL was reported for fin whales by Ohsumi (Kimura, 1957) and for sei whales by Gambell (1968), but the presence of a single CL does not necessarily indicate identical twins (e.g. Gambell found a foetus of each sex in a sei whale with one CL). Collet has found a single Graafian follicle with two eggs in *Delphinus*. This is relatively common in cats, humans and other mammals. Dizygotic twins have been identified by the presence of two CLs or because the foetuses were of different sexes.

An observation of twinning in a bottlenose dolphin in captivity suggested that the CL in dolphins is under local rather than systemic control. Gray and Conklin (1974) reported that a female bottlenose dolphin died one week after aborting one twin. Upon examination it was found that the CL for the aborted foetus had regressed, while that for the foetus *in utero* was still active. This is one of the few available observations on the regression rates for CLs.

In summary, it is believed that the mature delivery of twins is unlikely, as it is as yet unrecorded, and that typically either the calves are aborted or the female dies.

(6) *Vaginal calculi*

Vaginal calculi have been reported for a variety of cetacean genera, including *Stenella*, *Delphinus*, and *Lagenorhynchus*. In one *S. attenuata*, 13 vaginal calculi of calcium phosphate were reported, but their origin is unknown (Sawyer and Walker, 1977). Collet reported that she found calculi in 3 of approximately 30 stranded specimens in France. Sawyer and Walker summarized other calculi data. In some cases the calculi may be calcified semen or vaginal mucus, but in at least three cases calculi have been shown to contain bones from embryos (Benirschke, Henderson and Sweeney, this volume). The incompletely expelled foetus was located in the false cervix between the vagina and cervix in each case. The fate of this kind of calculus is unknown. It may be resorbed eventually, or it may remain in the false cervix for a long time. It is not known if the false cervix opens except during copulation. Walker reported a large calculus in a *Delphinus* with a large foetus. It is believed that the unusual structure of the dolphin reproductive system, especially the false cervix, contributes most significantly to the presence of these calculi, which in at least some cases may interfere with reproduction.

(7) *Other pathology*

Benirschke noted that cetaceans are remarkable in their lack of pathology in the reproductive system. The incidence of pathology is much less than that seen for humans or other terrestrial mammals. In addition to the granulomas from worms described above, two other pathologies were noted in the material available to the workshop:

(1) A granulosa cell tumour previously undescribed for cetaceans that was found by Marsh in a 34.5-year old *G. macrorhynchus*. The tumour did not have the infoldings of cavity remnants found in a typical corpus luteum, and showed a great proliferation of granulosa cells. This type of tumour is found in humans and can be induced in rats.

(2) Uncharacteristic calcifications were found in the ovaries of two *G. macrorhynchus* aged 44.5 years and 62.5 years. These abnormal calcifications may have resulted from old bleeding.

In addition, Collet reported finding 3 cases of hydramnios in 5 stranded females of *Delphinus delphis* and another in a stranded pygmy sperm whale, *Kogia breviceps*, and felt that this may have been the cause of death.

Differences in the incidence of pathology exist between genera, but it is unclear if the total occurrence of pathology within a population can be used as an index of the status of the population. Kasuya reported less pathology in *Stenella* spp. than in *G. macrorhynchus*, but there were apparently no differences between *S. attenuata* and *S. coeruleoalba*. It was suggested that the difference between genera may at least in part be explained by the difference in life spans. In humans and other terrestrial mammals, cancers, fractures and congenital abnormalities are seen more frequently than in animals with shorter life spans.

Pathologies in cetacean reproductive systems are apparently so unusual that any specimens are noteworthy and should be examined in detail. Part of the reason for the low rate of occurrence may be related to examiner acuity and experience. Greater attention to pathologies should be paid in the future.

III. MODELLING REPRODUCTION

(A) Terminology and assumptions

The group considered a draft glossary of terms used in modelling reproduction. After considerable discussion, it was concluded that there really is no accepted 'standard' terminology; many terms, for example, have been used differently in IWC assessment and management of whales than in terrestrial game management. Given this lack of consensus, the group decided that it would be impractical to try to develop a comprehensive glossary during the workshop. The problem of terminology remains, and the workshop recommends strongly that terms which might be interpreted in more than one way are fully defined whenever used. Some particular points brought out in the discussion are summarised below.

(1) *Density dependence*

It was agreed that 'density dependence' should be thought of as a general term relating to *some* specific resource, which is not necessarily area. The limiting factor could be, for example, abundance of food or of predators.

(2) *Pregnancy rate*

Frequently models assume pregnancy is synonymous with birth. Although this is not true, it is usually unimportant in practice, as the assumed juvenile mortality rate incorporates pre-natal mortality.

(3) *Age at first parturition*

The value of the mean age at first birth, used as a parameter in most models, is often estimated as the mean age at maturity plus the gestation period. This is appropriate, however, only if the first ovulation results in a birth. If it does not, the age of first birth should be increased.

(4) *Specifying intervals*

With the discrete-time models used for real populations, it is necessary in light of both the discrete intervals of our sampling and the tendency for seasonality in population dynamics, to specify when, with respect to the interval(s), the censuses which describe the population trajectory (or the vital rates which define the *per capita* dynamics) are to refer. Commonly, the census refers to the beginning of the interval, age class x refers to the sum of individuals aged $x-1$ to x at that time, survival rates refer to proportion surviving from one census to the next, and fecundities refer to the number of offspring censused (alive) at time $t+1$ per mature female in the appropriate age class censused at time t. Other sets of definitions are possible, but it is important to note that it is not necessarily innocuous to mix them.

(5) *Specifying assumptions underlying terminology*

It is unfortunately only very rarely that the elementary parameters for a population dynamics model can be estimated directly from feasible experiments or field programmes; what can be measured are certain population parameters, such as relative frequencies of individuals in different age classes or reproductive states. Various assumptions are then made (usually concerning age distributions and mortality rates in between censuses) depending on the particular instance, to enable one to compute the desired parameters from the available measures. Since the opportunities both for errors and inappropriate data manipulations are fairly extensive at this stage, all models should thoroughly describe how the dynamical parameters they employ were calculated from observed biological quantities, so that this process may be scrutinized. This is important because although the underlying mathematical theory of the computations may be standard, the improvisation carried out in each particular model may require some unravelling, and the reasonableness of the assumptions must be evaluated case by case.

(B) Current models

The participants in the workshop expressed a desire to examine a sample of the models currently being used in cetacean population assessment and management. Three approaches to modelling cetacean populations were reviewed, with emphasis placed on the role of reproductive rates as inputs to these models. The models presented were (1) the current [1981] sperm-whale management model used by the IWC (presented by Kirkwood), (2) the NMFS model for managing dolphins involved in the tuna fishery (presented by Smith), and (3) the IWC management model for North Pacific baleen whales (presented by Horwood).

(1) *The sperm whale model*

The IWC model for sperm whale dynamics (Allen, 1973) belongs to a large class of population models known collectively as age-structured models. With such models, a strict accounting is kept of the numbers of individuals estimated to be within each age class; in this case, age classes are given in one-year intervals. In addition, in the sperm whale model the numbers of males and females are both significant to population growth rates and are examined separately. At the core of this model is the simple updating relationship; the number of individuals in a given age class in a year is equal to the number of individuals in the previous age class one year earlier minus the catch from the previous age class during that year, all multiplied by the survival rate of that age class. The number of individuals entering the first age class is given by the number of mature females in the previous year times the birth rate of mature females.

The assumptions of this approach have to do with the functional form given to the age-specific survivorship and birth-rate parameters. Females are classified as either juveniles (0–2 years), sexually immature (3–9 years), or sexually mature (10+ years). Males are classified as either juveniles (0–2 years), sexually immature (3 to ~ 20 years), sexually mature (~ 20 to 24), or socially mature (25+ years). The first assumption used is that survival rates for all non-juvenile males and females are constant with age and through time. These rates are estimated from age samples from the catches. The second assumption is that the juvenile mortality rate is the same for males and females and is constant through time. This rate is estimated from a balance equation by assuming that, at unexploited equilibrium, the number of adult females dying in any year will equal the number of females being recruited into the adult population. Because pregnancy rates are used rather than birth rates, the estimates of juvenile mortality by this method will be biased; this will not, however, affect the results of the model.

All aspects of density dependence are incorporated into the assumptions about the functional form of the pregnancy rate.[5] Pregnancy rates are assumed to be equal for all mature females. These rates are assumed to be related to the ratio of the number of mature females in the population to the number of mature females in the unexploited population by a non-linear function. The maximum pregnancy rate is taken to be 0.25 and the minimum is taken as 0.20 (corresponding respectively to 4- and 5-year calving cycles). The degree of non-linearity was chosen so as to obtain a single-sex maximum sustainable yield level (MSYL) of 60% of equilibrium density. The pregnancy rates are also dependent on the number of socially mature males in the population. Once the number of socially mature males falls below some threshold, pregnancy rates are assumed to be linearly related to the abundance of such males. The number of males can thus strongly influence pregnancy rates if they fall below this threshold (IWC, 1981a, pp. 100–1).

It was emphasized that actual evidence for density-dependence in the pregnancy rate of sperm whales is insufficient to empirically determine relationships such as those assumed here. For most stocks, the estimates of population sizes are not sensitive to the form of the pregnancy model. However, estimates of replacement yields and MSY levels are very sensitive to the pregnancy model.

(2) *The ETP dolphin model*

The second example of a management model is that used by the United States National Marine Fisheries Service (NMFS) to determine the status of the dolphins which are involved in the tuna purse-seine fishery in the Eastern Tropical Pacific (ETP). Reproductive rates enter into two rather distinct models, which are both inputs to the management decision process. The first model involves the estimation of the ratio of current abundance to historical (assumed equilibrial) abundance of the populations. The second model involves the estimation of the MSYL of these populations. As currently mandated by US law, the classification of populations of marine mammals as 'depleted' is defined by population levels falling below MSYL (maximum net productivity level, or MNPL in NMFS' terms), hence both elements are required for management decisions.

The ratio of current to historical abundance is estimated by back calculating the abundance of dolphins in 1959 (the beginning of incidental dolphin mortality) from the abundance of dolphins estimated in the last aerial survey (1979). The back calculation can be thought of as a simple accounting exercise. The number of dolphins in a given year is calculated from the number in the next year minus the net recruitment into the population plus the mortality due to fishing in that year. Although reproductive rates do enter into this calculation as an element of the net reproductive rate, the model is quite insensitive to the actual functional form of this net reproduction relationship. It is relatively insensitive to the value chosen for the maximum net reproductive rate over the range of values (0–4%) considered in a recent stock assessment exercise (Smith, 1979). An example can be given for the offshore spotted dolphin: if the MSYL is assumed to be 0.65, the ratio of current to historic abundance would only change from 0.45 to 0.52 if the net reproductive rate were doubled from 0.02 to 0.04.

The net reproductive rate was assumed to be density dependent, and the specific functional form of this density dependence is of prime importance in determining the second element of the management decision processes, the estimation of MSYL for the species involved. The net reproduction function used in the above model is given by

$$\rho(N) = \rho_0\left(1-\left(\frac{N}{N_{1959}}\right)^{\zeta}\right) \tag{1}$$

The parameter ρ_0 in this equation is what can be referred to as a phenomenological parameter. Simply stated, this means that this parameter is a composite of many processes which for convenience have been lumped into a single term. As is usually the case, these processes were lumped because they could not be measured separately. Roughly, ρ_0 can be thought of as the difference between the gross annual birth rate and the gross annual death rate in a population that is growing at its maximum rate. The parameter ζ affects the shape of the density dependence. Values of this parameter can be chosen so as to obtain MSYLs from any desired fraction of the equilibrium population levels (Smith, 1979). The assumption here that is of concern to the workshop is that reproductive rates and/or survival rates are density dependent. Currently there is no solid evidence that either of these life history parameters of ETP dolphin are density dependent.

(3) *The North Pacific baleen whale model*

The third management model presented was that used for the North Pacific large whale populations and for the Southern Ocean species before the interspecific relationships were recognized. Unlike the sperm and to a lesser extent the current BALEEN (Allen and Kirkwood, 1979) models, but similar to the above dolphin model, this model does not involve detailing age structure. The number of whales in the component of the population recruited to the fishery is given by those surviving from the previous year plus the incoming recruitment (Breiwick, 1978).

The natural survival rates are assumed to be constant for all population densities. Recruitment rates are assumed to be density dependent and the functional form of this is modelled in a similar way to the net reproductive rate in the dolphin model.

$$N_{t+1} = N_t(1-M)+\left(r_0\left(1-\left[\frac{N_t}{N_0}\right]^{s}\right)+M\right)N_t$$

Where N_t is the recruited population size at time t, M is the proportional mortality and (r_0+M) is the maximum gross recruitment rate. Often M is estimated from the age composition of a catch taken in the early years of the fishery and r_0 and s are given by assuming that MSY is 4% of the population size at 50–60% of the initial population size. If exploitation has existed for a shorter time than the age of recruitment then exploitation will have no effect on current levels of recruitment (similar to that described for sperm whales). In this case a modified DeLury estimation technique can be used (Chapman, 1974; Tillman and Grenfell, 1980).

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[5] Editors' note. There has been considerable discussion in recent years over the appropriateness of this aspect of the model, e.g. see IWC, 1980, pp. 67–9, 111–12; IWC, 1982a, p. 73; IWC, 1983, pp. 687–8

(C) Density dependence

As evident from the examples discussed above, reproductive rates in cetaceans are often assumed to be density dependent in management models. In none of these examples do sufficient data exist to actually estimate the functional response of birth rates to changes in population density. In some cases, there is no direct evidence at all for density dependence in reproductive rates. A question was therefore directed to the participants in the workshop: 'What direct evidence is there for density-dependent responses in reproductive parameters for Cetacea?'

(1) *Pregnancy rate or calving interval*

The evidence for density dependence in reproductive rates of Southern Hemisphere fin whales was examined in two papers presented in the Symposium (Beddington and Grenfell, this volume; Mizroch and York, this volume). Although these reports were not in agreement, both included important points for consideration which should be kept in mind when reviewing the evidence for density dependence that follows. First, apparent pregnancy rates may be correlated with other factors such as the area, season and methods of sampling; hence, care should be taken to properly stratify samples. Second, by considering only the mean pregnancy rates, significant patterns in the residuals can be missed. Third, analyses of density dependence should not be limited to correlations between vital parameters and absolute abundance: the response of prey species may also be important, as well as competition and other factors. Finally, since pregnancy rates can be dependent on the age of females, care should be taken to ensure that changes in length frequencies do not confound attempts to examine density dependence.

Evidence for density dependence in eastern Pacific dolphins was discussed in two symposium papers (Hester, this volume; Smith, this volume). Hester showed an extremely rapid decrease in apparent pregnancy rates of spotted dolphins which occurred during a period of decreasing incidental mortality. Possible implications of this are that the population was increasing very rapidly during this time, or that sampling bias changed during this time, or both. There are, however, no data on changes in population size during this period. Smith (this volume) showed evidence of a higher gross annual reproductive rate in those populations of spinner dolphin that had been subject to greater reductions in population size as a consequence of tuna net mortality. Possible problems with these results are, again, sampling bias and the differences in the habitat of the three populations. Another problem is the number of fitted parameters involved in the analysis.

Positive evidence of density dependence in pregnancy rates was cited at the workshop for two other odontocetes. Best (1980) presented data for sperm whales. Kasuya (this volume) showed that the apparent pregnancy rate of striped dolphins changed through time in an exploited stock, however, the area fished expanded during this time period.

Two cases were pointed out for which evidence for density dependence might have been expected. Sergeant reported the case of long-finned pilot whales in the western North Atlantic, where approximately 50% of a local stock was removed and no change was seen in apparent pregnancy rates. The time period of this study was, however, very short. Reilly mentioned that although the California gray whale stock is apparently growing, insufficient data exist for determining any consequential change in pregnancy rates.

Mitchell cited one case of apparent inverse density dependence in pregnancy rates, in Atlantic fin whales (Mitchell, 1974). Apparent pregnancy rates were lower in one stock (heavily fished over a long period, from Dildo and Williamsport, Newfoundland) than in another, less-heavily exploited stock (fished from Blandford).

(2) *Age at attainment of sexual maturity in females*

Perhaps the strongest evidence for density dependence in reproductive rates is a decrease in the age at sexual maturity of females as population size decreases. It was noted that in several cases (Lockyer, this volume), although the average age at sexual maturity did decrease with population density, the average length at sexual maturity did not change, implying changes in growth rates.

The only evidence cited for odontocetes of a reduction in the age of sexual maturity was for striped dolphins. Kasuya (this volume) documented that the age at which 50% were mature in an exploited population of this species decreased from 9.7 to 7.4 years during the period 1955–1970. Sexual maturity was inferred from ovarian activity.

Two sources of data were used to show a reduction in the mean age at sexual maturity in Southern Hemisphere fin and sei whales (Lockyer, 1972; 1974; 1977a; 1979). First, age at sexual maturity was inferred from ovarian activity and number of earplug laminae. Second, the onset of ovarian activity was found to be correlated with a reduction in the thickness of the annual layers in the earplugs of these whales (Lockyer, 1972; 1974). The first method was used to calculate the age at sexual maturity for both recent harvests and those in the 1950s. Earplugs were not, however, collected during the earlier history phase of fin and sei whale exploitation. The second method used therefore was to back-calculate the age at sexual maturity of females that had matured many years prior to the time when earplugs were first collected. Three possible problems were identified with this approach. The average age of sexual maturity for the most recent years will tend to be biased downward because those females that would mature late have not yet come of age. Second, early-maturing animals may be under-represented in the earlier cohorts if their mortality rates are higher. This would also lead to a downward bias. Third, an early age of sexual maturity would not result in increased birth rates if younger-maturing animals had a lower survival rate. The order of decline in age at first maturity is from about 10 years to about 6–7 years in fin whales and from about 11 years to about 8 years in sei whales.

There is one case where the age at sexual maturity has shown resource dependence. Although the Southern Hemisphere minke whale has only recently been exploited, its food supply might be expected to have increased as a result of the depletion of the great whales.

Indeed the age at sexual maturity has apparently decreased in this species (Lockyer, this volume).[1]

(3) *Percentage simultaneously lactating and pregnant*

The length of the calving interval in cetaceans could be reduced if they were capable of ovulating and becoming pregnant while still lactating. A change in the proportion of pregnant and simultaneously lactating females may therefore indicate a density-dependent response. At least since the establishment of the IWC in 1946, protection has been granted to animals accompanied by calves, which effectively means that for all large whale species, lactating females are protected – hence detecting any change would be difficult. Mitchell (1974) showed that for fin whales in a previously heavily exploited population, 6% were both pregnant and lactating, as opposed to 0–2% in a stock only recently fished. No other evidence was cited for density dependence in this parameter. Kasuya noted that the pregnant and lactating category was limited to those spotted dolphins less than 20 years of age and striped dolphins of less than 35 years in populations off Japan. Perrin stated that this category was uncommon in dolphins of the ETP. No evidence for density dependence was cited for any of these dolphin species.

(4) *Mean age in the population*

If the rate of population growth is density-dependent, the equilibrium age structure of a population will typically vary with density. For example, if calf survival is the only density-dependent factor, then as a population increases, the mean age in that population will also increase. If only adult survival were density-dependent, the mean age would decrease. For cetaceans, no evidence was cited for a change in age structure associated with a change in density. This kind of change would be difficult to detect in exploited species since most harvests show age specificity.

It was pointed out that in the case of small odontocetes, difficulty in ageing old animals has sharply limited the use of age-structure data in modelling population dynamics.

(5) *Population growth in depleted populations*

These are essentially two approaches to determining density-dependent response of populations. The above discussions have dealt only with the deductive approach: what effect does density have on the life-history attributes of a population? An alternative approach would be to ignore the details and look for the gross effect of density dependence: a change in the growth rate of a population. At equilibrium, net growth rates are zero. If growth rates increase in an exploited population, this is evidence for density dependence. The choice of approaches will depend on the types of information that can be gathered and the precision of each.

Evidence for positive growth rates in depleted stocks was cited for two species of baleen whale: gray whales from shore counts (Reilly, this volume) and right whales from shore and aerial counts (Mermoz, 1980; Best, 1970; 1981; Best and Roscoe, 1974).

(6) *Additional comments*

(*a*) *The problem of 'noise'*. Any population which persists must, as a mathematical certainty, exhibit some density dependence in its population dynamics. This mathematically necessary property does not establish what time lags the density dependence operates on, which components of the life history display the density dependence, or the functional form of the density dependence. The biological problem lies in discovering the mechanism by which the density-dependence occurs, and the associated statistical difficulty lies in demonstrating this from a limited and noisy data base. It will often be the case that density dependence cannot be 'demonstrated' nor can statistically defensible values be estimated for the parameters of the governing dynamics of the population, even though it is certain, on other grounds, that the dynamics are indeed density dependent. For similar reasons, it may only be possible to justify parameterization of a linear model for density dependence, but this is more in the way of a conventional linear approximation than an assertion that the response really is linear.

(*b*) *The dangers of extrapolation*. The estimation of parameters for a density dependent model of population growth is an empirical exercise in curve fitting. Thus some data will be available concerning population growth rates at a set of densities and parameterization of the model will consist in fitting some function to the observed growth-density relationship. Once the parameters of the function have been fitted, it becomes possible to compute a predicted population growth rate at any density, but the security of these predictions will, of course, deteriorate as the densities to which they refer depart from those densities bracketed by the data which were used in the actual curve fitting. For example, it is possible to compute the theoretical density at which the fitted growth curve yields a zero value (and call this the 'carrying capacity'), or to compute the percentage growth rate associated with a zero density (and call this the 'maximum reproductive rate'), but these values should not be taken seriously if the data were remote from these particular external densities. The temptation to be seduced by extrapolations is greater when the parameters of the equation used are conventionally given names such as 'k' or 'intrinsic rate of increase' which seem to denote some biological reality that in fact does not exist.

IV. DATA AND SPECIMEN NEEDS FOR STOCK ASSESSMENT AND MANAGEMENT

(A) Information needs

(1) *General comments*

The ultimate use of sampling data is in the fitting of bio-mathematical models to aid us in understanding what is happening to the particular stock. Simple models usually do not use all the types of data that are or should be collected, and more complex models are needed to incorporate behavioural and physiological data and information on life history in terms of ecological interactions.

In stock assessment models it is important to estimate all the demographic characteristics of the population under study, but in most instances knowledge of many of these is limited. Often the effect of the characteristics is multiplicative e.g. pre-natal mortality and juvenile mortality; thus if only one is known; the outcome, as the product of the two, is also unknown. In many instances therefore, the accurate estimation of a particular parameter may not help in the short term, at least in terms of stock assessment. However when additional problems are resolved, our knowledge of the population demography will be greatly enhanced. Therefore, it is essential to maintain long term basic research, for only this will ultimately provide the knowledge to develop correct population models.

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[1] Editors' note. A recent workshop (IWC, 1984b) discussed the available evidence for a decline in age at sexual maturity in the Southern Hemisphere minke whale but was unable to conclude whether or not such a decline had taken place. The discussion was also relevant to other species.

In conclusion, it is important to collect as much biological data as possible, even if the information provided may not be 'necessary' direct input for the population model currently being used; such data may, for example, provide a check on the internal consistency of these models as well as serve to develop a realistic model of a species' demography in the long run.

(2) *Some specific needs*

In addition to the obvious need for data on age-specific pregnancy and maturity already discussed earlier in this report, other, less obvious needs can be identified.

(*a*) *Age composition of the catch.* Cohort-analysis techniques are available which can give good estimates of past population size (although not for very recent years) and an estimate of recruitment rates independent of information on pregnancy and juvenile mortality rates. For these techniques it is important to have accurate information on the age structure in the catch over a number of years. Various authors (e.g. Cooke and Beddington, 1982; Cooke and de la Mare, 1983; Shirakihara, Tanaka and Nakano, 1983) have recently described population estimation techniques for sperm whales which utilize the age and length distribution in the catch.[7] The exploitation history of most sperm whale stocks has been such that the estimates of population sizes from the start of exploitation to the present are little affected by recent possible changes in reproductive performance. Consequently, independent comparisons of observed and predicted pregnancy rates may be possible.[8]

(*b*) *Sex composition of the catch.* In certain fisheries the sex ratio in the catch varies significantly from 1:1. In some of the minke whale fisheries, for example off Norway, there is a preponderance of females in the catch in certain areas and at certain times (Christensen, 1975; 1979). In other fisheries, notably for sperm whales, where the males are considerably larger than the females, a preponderance of males is caught. The effect of these removals on reproduction may depend on the degree of reduction of mature whales (see description of the sperm whale model above). Further information on the social behaviour of individual species is essential if the effect of the distortion of the sex ratio is to be fully understood.

(*c*) *Calf counts.* In several sighting surveys, the proportion of calves to adults has been much lower than might be expected from current population models (IWC, 1981b). It is important that further work is undertaken to determine if these proportions are truly representative of the population or if they are the result of survey problems (e.g. segregation of cow/calf pairs, or differential sightability of adults and calves).[9] Payne (1984) reported that for right whales in Argentina, three separate breeding populations use the Peninsula Valdes area in separate years. This needs to be taken into account in right whale surveys in other areas.

(B) Data Sources and Sampling Problems

Discussions on data sources and sampling problems in the estimation of cetacean reproductive parameters focused on the relationship between what is actually measured in field samples and the corresponding population values needed for stock assessment and management. Several distinct sampling methods were identified, each possessing its own set of sampling problems.

(1) *Samples from commercial catches*

(*a*) *Large whales.* By far the greatest source of information on cetacean reproductive parameters lies in catches taken from stocks that are exploited in a directed or incidental fishery.

Since 1946 the following data have been routinely collected from each whale caught in accordance with The International Convention for the Regulation of Whaling: species, length, sex, position and date of capture, presence or absence of foetus, length and sex of foetus if possible, and whether lactating. More recently the requirements have been expanded to include the collection, wherever possible, of material for ageing (either earplugs or teeth), of ovaries and of testes weight or at least a sample of testis tissue, although much of this was already collected under national programmes. In addition, data on school size and on sightings of all species (including those protected) are included in the effort forms which each catcher boat must complete.

While very large samples have been taken from commercial catches, there are a number of problems in converting sample estimates of reproductive parameters to the population estimates. Most of them relate to the degree in which the samples are representative of the whole population. For large whales, IWC regulations prohibit the taking of animals accompanied by calves, with the result that the 'lactating' segment of the mature female population is largely missing from samples. Consequently, apparent sample pregnancy rates overestimate true pregnancy rates. Allowance for the under-representation of lactating females has been addressed by Horwood, Donovan and Gambell (1980) and Martin (1982).

Even if no specific segment of the population is absent from catch samples, several reasons can be identified for the possible failure of catches to be representative even of the segment of the population in the area from which samples were taken. By their nature, most fishing methods are selective. In the large cetacean fisheries, it was noted that deliberate selection of large animals could lead to bias in the samples.

A problem common to all catch samples is that due to

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[7] Editors' note. For a discussion of these see IWC, 1983.

[8] Editors' note. Some attempts to do this have been made e.g. see IWC, 1981a, pp. 79–80; IWC, 1983, p. 691.

[9] Editors' note. This problem is discussed in IWC, 1984a.

changes in whaling/fishing grounds with time, samples are taken from different segments of the population at different times. Such problems have been noted for Antarctic fin whales by Mizroch and York (this volume). Time series of apparent pregnancy rates for North Pacific sperm whales have been partially confounded by changes in whaling grounds over time (e.g. see IWC, 1981b, p. 689).

It is apparent from the above discussion that while very large samples are available from commercial catches, there are a number of difficulties in using these data in stock assessment. Clearly, nothing can be done about the historical data. In discussing possible means for minimizing the bias in future samples from catches, several members suggested that it may be possible to increase the representativeness of the catch samples by requiring allowable catches to be taken over a wide area. Changes in methods of handling carcasses may reduce the incidence of lost foetuses. It was recognized that such suggestions may have a significant impact on profitability of the industry. Lockyer reported that new methods were being investigated in Iceland for determining whether captured mature females were pregnant in cases where the foetus had been lost. The methods involve histological study of the endometrium and assay of hormone levels in blood and urine (see Sigurjónsson and Kjeld, 1982).

(*b*) *Directed small cetacean fisheries:* Mitchell (1975) and subsequent reports of the IWC Sub-Committee on Small Cetaceans (IWC, 1976–1982) reviewed the known small cetacean fisheries of the world. The following additional information on data collection in certain fisheries was available to the workshop.

(i) *Japan*. Ohsumi reported that in certain prefectures a licence from the local government is required for small cetacean hunting, and catch statistics are systematically collected. In other prefectures, no licence is required, but statistics are collected. National research programs have been initiated on the populations of dolphins and other small cetaceans taken at Iki Island and in other directed fisheries. Kasuya and Marsh (this volume) have reported on the drive fishery for short-finned pilot whales and Kasuya (this volume) has reported on the exploitation of striped and spotted dolphins in Japanese coastal waters. Problems of representativeness exist here also. Miyazaki reported that in the striped dolphin fishery there were differences in apparent pregnancy rates between samples drawn from the harpoon fishery and the 'driving' fishery.

In fisheries for small cetaceans that segregate by age and sex (even when there may be no specific bias in catch samples), samples taken from individual schools show greater variability between than within schools. For example, Miyazaki and Nishiwaki (1978) found that apparent pregnancy rates in schools of striped dolphins varied from 0 to 94.4%. In such circumstances it is necessary to take samples from as many schools as possible.

(ii) *Canada*. Sergeant reported that there are no data collection requirements for the white whale and narwhal fisheries other than species and number caught, but some data on sinking-loss rate have been collected by (government and non-government) scientists.

(iii) *Greenland*. Larsen reported that no data beyond species and numbers caught are collected from the small cetaceans taken in Greenland.

(*c*) *Incidental takes*. Incidental takes of cetaceans have been reviewed extensively in recent IWC Reports (IWC, 1976–82). Additional information made available at the workshop follows.

(i) *ETP tuna fishery*. Hammond reported that although there are no obligatory requirements under IATTC (Inter-American Tropical Tuna Commission) regulations, the following data are routinely collected from incidentally killed dolphins by IATTC and NMFS scientific observers (on board US vessels): species, sex, length, reproductive tract of females, testis sample (including epididymis), sex and length of foetus (small foetuses are brought back in formalin), teeth. IATTC observers on non-US vessels, however, do not currently collect specimen material. Although the percentage varies considerably by year, this programme covers about 25% of the estimated total kill on observed cruises. It is noted that younger animals and lactating females are more frequently killed in 'sets' on tuna and dolphin schools that result in lower total mortality than in those that result in high mortality.

(ii) *Other incidental catches.*

People's Republic of China – Chen reported that although it is against Chinese law to catch river dolphins, they are sometimes killed accidentally during fishing operations. Chen reported about 10 specimens of *Lipotes vexillifer* and more than 20 of *Neophocaena phocaenoides* have been examined and the reproductive organs analysed by the Institute of Hydrobiology of the Academica Sinica (Chen, Liu and Lin, this volume).

Brazil – *Inia geoffrensis* and *Sotalia fluviatilis* are caught incidentally in fisheries in the Central Amazon, and where possible reproductive tracts (Best and da Silva, this volume) stomach contents, parasites, etc. are collected. Tucuxis (*Sotalia*) are occasionally taken near the coast and used for fish bait, and the increasing use of drifting gillnets may result in an increase in the incidental kill in the Amazon. Franciscanas, *Pontoporia blainvillei*, are also captured in the coastal waters of Rio Grande do Sul in fishing nets; over 200 have been collected and are under study.

Japan – Ohsumi reported that Dall's porpoise, *Phocoenoides dalli*, are taken incidentally in the Japanese gillnet fishery in American waters of the North Pacific. As part of the research programme, scientists on board certain vessels collect reproductive organs, stomach contents, whole animals and other specimens. There appears to be bias towards pregnant females (over 90% in the samples) and an over-representation of younger males.

Denmark – Harbour porpoises, *Phocoena phocoena*, caught incidentally in fisheries in Danish waters are sampled for studies of reproduction, parasite infection, etc. by the Institute for Physiology of the University of Odense.

(2) *Direct counts from surveys*

An alternative method to sampling from commercial catches for estimating the proportion of calves in the population is the use of direct counting techniques through aerial or ship-based surveys or coastal censuses. Where it is possible to cover most, if not all, of the range of a stock, or if the entire stock migrates past a single point, survey techniques may provide much more representative data than those available from catch samples. Cliff-top or aerial surveys aimed at least in part at obtaining calf counts have been carried out for right, humpback, gray and bowhead whales. Several participants commented that for humpback and bowhead whales, much lower calf/adult ratios had been observed in these surveys than might have been expected. Much higher ratios had been observed for southern right whales off South Africa (Best, 1981; IWC, 1981b). Other participants, citing Payne's (1984) suggestion that there may be 3 separate groups of calf-bearing females off Peninsula Valdes, queried whether the estimates obtained by Best for the waters of southern Africa may be too high (Best, 1970; 1981; Best and Roscoe, 1974).

It was recognized that it is often difficult to obtain full counts of calves from shore-based observations. For example, for Alaskan bowheads Braham reported that the gross recruitment rates estimated from ice camp surveys (1–3%) were generally lower than estimated from aerial surveys (2–5%) (Marquette, Braham, Nerini and Miller, 1982; Cubbage and Rugh, 1982).[10] In this context, much interest was expressed in the application of aerial photogrammetric techniques described by Perryman, Scott and Hammond (this volume) for obtaining calf percentages and length distribution. They have developed a technique for measuring small cetaceans from vertical aerial photographs. Preliminary analyses of some of the data have revealed that modal length distributions can be seen which may correspond to 6-months age groups up to an age of 1½–2 years (i.e. during the linear phase of the growth curve) and may therefore enable estimates of first-year mortality to be obtained. Such techniques may be particularly useful for coastal species.

It was noted that use of aerial survey techniques has been restricted largely to coastal cetacean species, because of the high cost of farther-ranging surveys, such as that carried out in the eastern tropical Pacific (Smith, 1979). It was pointed out that in view of the diving synchrony of sperm whales, aerial photographic surveys may be particularly valuable under appropriate circumstances.

(3) *Strandings*

The group agreed that stranded animals are a special and probably unrepresentative segment of a population, particularly single stranded animals. The causes for strandings are still unknown. A common observation in mass strandings is an apparent over-representation of very young and much older animals, as well as unbalanced sex ratios, although it was reported by Sergeant that stranded groups of *Globicephala* spp. and *Pseudorca* appear to resemble schools driven ashore in fisheries in age and sex composition. It was agreed that in most cases it is difficult to use estimates of reproductive parameters obtained from stranded animals for stock assessments. A possible exception noted is mass strandings of whole schools of predominantly sperm whale cows and calves. However, when a species is not taken in any directed or incidental fishery, stranded animals represent the sole source of samples from which reproductive data can be obtained. Many participants commented on the difficulty in obtaining biological samples from mass strandings in isolated areas, and noted that it took many years for adequate sample sizes to be accumulated. In view of this, it is important that standard procedures be adopted in collecting biological data from mass strandings of cetaceans. 'Strandings networks' such as have been established in the US, the UK, Canada, France and Australia have proved extremely valuable in this regard. It was urged that tooth or earplug samples for ageing be taken from stranded animals.

(4) *Individual-animal studies*

The final category of samples that may provide information on cetacean reproductive parameters is that of studies on individual animals. These fall into two types: captive-animal studies and long-term studies of population of identifiable individuals in the wild.

Captive-animal studies have included monitoring of births for individual females, measurement of reproductive hormone levels and observations of social behaviour coupled with measurements of reproductive-hormone concentrations in dolphin colonies dedicated to such research. The information from records of captive births is of value in determining reproductive seasonality or, in some cases, age of first reproduction, but complete records of the female's tankmates are necessary to obtain data on other parameters. Concentrations of reproductive hormones in either serum or plasma have been measured for a number of delphinid species in attempts to determine reproductive condition. The most extensive measurements have been made for *Tursiops truncatus* (Harrison and Ridgway, 1971; Judd and Ridgway, 1977; Kirby and Ridgway, this volume; Richkind, 1977; Sawyer-Steffan and Kirby, 1980; Sawyer-Steffan, Kirby and Gilmartin, 1983) *Stenella longirostris* (Wells, this volume) and *Delphinus delphis* (Kirby and Ridgway, this volume). Kirby reported that hormone information is also available from studies of single live specimens of *Globicephala macrorhynchus* and *Orcinus orca* and from occasional measurements from a few specimens of *Lagenorhynchus obliquidens* and *Delphinapterus leucas*. Measurements of concentrations of progesterone and oestrogens in female delphinids have generally shown that multiple ovulations within a given season are possible, as are seasons without ovulations, and spontaneous ovulations occur in at least some delphinids. Hormonal monitoring is also yielding information on gestation length for several of these species. Seasonal changes in testosterone production in male delphinids have also been recorded.

Detailed behavioural observations in conjunction with regular blood sampling have been made for three species of delphinids in captive colonies. Kirby has closely observed 1 male–2 female *Tursiops* combinations while monitoring steroid concentrations. Kirby and Ridgway observed captive female *Delphinus delphis* over a period of two years while regularly measuring progesterone and oestrogen. Wells observed a captive colony of *Stenella longirostris* and noted changes in association and interaction patterns of individuals correlated with changes in reproductive hormone concentrations.

Captive animals whose entire reproductive histories are known may eventually also contribute greatly in interpretation of the reproductive history via examination of ovaries after death.

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[10] Editors' note. The most recent discussion of this problem is included in IWC, 1984a.

In recent years, declining catch limits set by the IWC for large cetaceans and increasing national controls over small cetacean fisheries have resulted in samples from commercial catches becoming increasingly difficult to obtain. Thus greater emphasis must be placed on gathering data on population reproductive rates and parameters from free-ranging animals. Longterm studies of populations in which individuals have been reliably identified on a repeated basis have been carried out for coastal populations of both baleen and toothed whales. Observations of recognizable individuals over several years can provide information on calving cycles, recruitment and loss from the population, and the relative position of individuals in the social/breeding structure of the population. Payne has identified over 500 right whales, *Eubalaena australis*, off Patagonia over the last ten years and has constructed reproductive histories for his indentifiable females. Glockner-Ferrarri (this volume) and others have been able to identify several hundred humpback whales from colour patterns, 'facial' grooves, and scars, and have been able to follow a number of identifiable females through several breeding seasons on their wintering grounds. Bigg, Balcomb, and others have been monitoring populations of killer whales, *Orcinus orca*, in the northeast Pacific over the last ten years. They have been able to identify nearly every individual in the populations, and have determined the sex of most of the population members (IWC, 1982). Wells reported that Norris and Dohl began identifying individuals from a population of *Stenella longirostris* off Kona, Hawaii over ten years ago. Norris, B. Würsig, M. Würsig, Wells, and others have continued the observations of this population since 1979, and at present can identify nearly 200 individuals, including females with calves. Irvine, Wells, and Scott have been working with a marked population of *Tursiops truncatus* off the west coast of Florida since 1970 (Irvine, Wells, Scott and Kaufmann, 1981). They tagged approximately half of the resident population, thereby obtaining information on the approximate age and sex of those identifiable individuals, and identified much of the rest of the population from natural marks, allowing the construction of reproductive histories for identifiable females over the last eleven years in some cases. As techniques for individual recognition from natural markings become better developed and more widely applied, much of the requisite information for assessment of populations that were previously inaccessible should become available. However, it must be recognized that the application of such techniques to oceanic populations may be extremely difficult if not impossible. In addition, capture/tagging/sampling/release programmes such as those of Irvine *et al.* (1981) can (a) provide much information on the age/sex structure of a population (particularly for a sexually non-dimorphic species), (b) produce physiological and reproductive profiles for recognizable individuals on a long term basis, (c) identify population differences, and (d) potentially identify the relative contribution of particular males to calf production within populations through analysis of genetic characteristics as has been attempted by Duffield, Odell, Asper, Searles, Evans, Finley and Fraker (this volume).

V. LITERATURE CITED

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VI. APPENDICES

Appendix A

AGENDA

1. Opening business.
    - (*a*) Introduction
    - (*b*) Adoption of agenda
    - (*c*) Adoption of schedule
    - (*d*) Confirmation of appointments
        - (i) Discussion leaders
        - (ii) Rapporteurs
        - (iii) Laboratory-demonstration coordinators
    - (*e*) Review of conference documents
2. Terminology of reproductive morphology and physiology.
    - (*a*) Group discussion
    - (*b*) Laboratory demonstrations
3. Interpreting ovarian scars.
    - (*a*) Group discussion
    - (*b*) Laboratory demonstrations
4. Current models of reproduction.
    - (*a*) Terminology and concepts – group discussion
    - (*b*) Testing hypotheses inherent in current models and management
5. Sampling problems – group discussion.
6. Comparative morphology of reproductive system.
    - (*a*) Laboratory demonstrations
    - (*b*) Group discussion
7. Data and specimen needs for stock assessment and management – group discussion.
8. Pathology of the reproductive system.
    - (*a*) Laboratory demonstrations
    - (*b*) Group discussion
9. Collection, storage and preparation of reproductive materials – group discussion.
10. Discussion of additional topics.
11. Write and review report of the workshop.

Appendix B*

TERMINOLOGY OF FEMALE REPRODUCTIVE MORPHOLOGY AND PHYSIOLOGY

(1) Morphology of the cetacean ovary

The external appearance of the ovaries of various cetaceans have been described and/or figured. Harrison (1969) and Harrison, Brownell and Boice (1972) summarize the relevant literature. Subsequent papers include those of Brodie (1972), Harrison (1972), Harrison and Weir (1977), Harrison and McBrearty (1973–74, 1977), Harrison, Bryden, McBrearty and Brownell (1981), Collet and Harrison (1981) and Marsh and Kasuya (this volume).

The ovary, like several other visceral organs, is basically composed of a cortex and medulla. The larger cortex contains most of the active cell types and tissues, the most important of which are the follicles with their oocytes, the corpora lutea, corpora albicantia and corpora atretica (each of which is considered separately below), the interstitial cells supported by stromal connective tissue, nerves, and lymph and blood vessels. Surrounding the cortex is a dense connective-tissue capsule or tunica albuginea, which is itself positioned under the covering 'germinal' epithelium.

The medulla consists mainly of dense connective tissue and larger blood vessels, although interstitial cells, hilar cells and structures of the rete ovarii are also found. Fisher and Harrison (1970), Harrison (1949; 1972), Harrison *et al.* (1972), Harrison and McBrearty (1973–74) have briefly described the rete ovarii of various odontocetes.

(2) Follicular development (Fig. 1)

'The follicle consists of the oocyte and its envelope which is composed of cells and an outer membrane. During follicular development the morphology changes as the oocyte and the surrounding cells differentiate' (Peters and McNalty, 1980).

The primordial follicle consists of a small oocyte, a single layer of granulosa cells and a basement membrane. Its appearance and size change little with advancing age. The primordial follicles represent the pool from which all follicles emerge.

The preantral (secondary) follicle is characterized by an oocyte that is in the growth phase with one or more layers of granulosa cells surrounding it. The wall of the follicle differentiates into two layers, the theca interna and theca externa. The transition from a preantral to an antral (tertiary, vesicular, Graafian) follicle is gradual and continuous. As the granulosa cells multiply, there is concomitant increase in the production and accumulation of fluid leading to the development of a follicular cavity or antrum.

As ovulation approaches, the (primary) oocyte resumes meiosis. After a reduction division, one set of homologous chromosomes remains in the cell, which is now called a secondary oocyte. A marked expansion of the whole follicle occurs shortly before ovulation and it bulges from the ovarian surface. In order to allow the secondary oocyte to exit, a localized part of the wall of the ovary and that of the follicle has to disintegrate. At ovulation, the secondary oocyte is released from the follicle and enters the oviduct. In cetaceans, ovulation is usually recognizable by the presence of a stigma, a scar on the surface of the ovary resulting from damage to the tunica albuginea and 'germinal' epithelium at ovulation.

(3) Follicular atresia and the development of corpora atretica

Coupled with the normal follicular development cycle is the concurrent normal phenomenon of follicular atresia,

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* Cited references are included in the Literature Cited section of the main body of the report above.

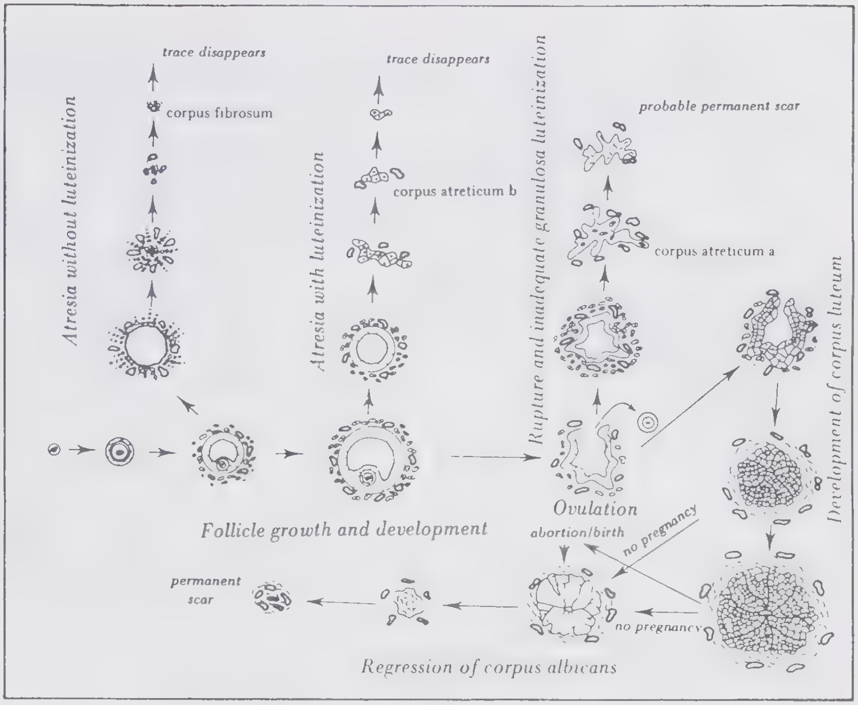
trace disappears
corpus fibrosum
Atresia without luteinization
trace disappears
corpus atreticum b
Atresia with luteinization
Rupture and inadequate granulosa luteinization
probable permanent scar
corpus atreticum a
Development of corpus luteum
Ovulation
Follicle growth and development
abortion/birth
no pregnancy
permanent scar
no pregnancy
Regression of corpus albicans

Fig. 1. A schematic representation in the form of a flowchart of the follicular changes occurring in a cycling cetacean ovary. It is also possible for a follicle to form an 'accessory' corpus luteum without releasing the egg. Some large antral follicles may also persist as cystic follicles. In this case macroscopically-detectable luteal tissue does not develop.

which is not necessarily simply a degenerative process. This metamorphosis of the follicle wall into a different kind of probably functional tissue occurs without ovulation as a normal and essential event in the ovarian cycle (Weir and Rowlands, 1977). Atresia gives rise to secondary interstitial tissue (usually considered difficult to find in cetaceans (Harrison and Weir, 1977), an exception being *Pontoporia blainvillei* (Harrison *et al.*, 1981)), or to accessory corpora lutea, both of which may be hormonally active (Weir and Rowlands, 1977). Relatively few Graafian follicles ovulate, many more become atretic.

Follicles may become atretic at any stage of their development (Byskov, 1979). Little is known about the atresia of small follicles, as this may not modify the macroscopic or microscopic structure of the ovary. However, the atresia of medium and large follicles is conspicuous and presents a variety of appearances depending on the stage of the follicle at the time it begins. In medium-sized follicles, atresia usually occurs without luteinization, i.e. without accumulation of lipids in the granulosa or theca cells. Small corpora fibrosa (Marsh and Kasuya, this volume) are derived from the basement membrane of atretic medium-sized follicles. These fibrous bodies are probably slowly resorbed; otherwise they would accumulate in far greater numbers than are seen in the ovaries.

Atresia of Graafian follicles of various sizes often progresses via different stages of luteinization. Lipid accumulation usually starts in the granulosa cells close to the basement membrane and in the cells of the theca interna. As atresia continues, the granulosa cell numbers become reduced by lysis and phagocytosis with concomitant collapse of the follicle (Byskov, 1979). During the atretic differentiation few thecal cells become necrotic. Rather they hypertrophy and accumulate lipid droplets, undergoing a type of 'fatty' degeneration. The resulting lipid is usually pale yellow at first and readily soluble in fat solvents but gradually oxidizes, becoming darker and more insoluble. The resulting structures persist for some time but usually not indefinitely (Marsh and Kasuya, this volume).

Lutealized (luteinized) follicles have been described in the ovaries of several cetaceans. Different terms have been used by various authors to describe different stages in the development and regression of these bodies as follows: corpora lutea atretica (Best, 1967); atretic follicles (Zimushko, 1970); unruptured lutealizing follicles (Harrison and McBrearty, 1973–74); luteinized follicles (Sergeant, 1962; 1973); atretic lutealized follicles (Harrison and Ridgway, 1971; Harrison, 1972; Harrison *et al.*, 1972); atretic corpora (Zimushko, 1970); yellow bodies (Laurie, 1937), corpora atretica (Laws, 1961; Kasuya, Miyazaki and Dawbin, 1974; Collet and Harrison, 1981; corpora atretica *b* (Best, 1967; Marsh and Kasuya, this volume), or corpora albicantia type 5 (Perrin, Coe and Zweifel, 1976). Most authors have not included them in counts of corpora albicantia; an exception being Perrin *et al.* (1976). We suggest that in future they should be called corpora atretica *b*. (Corpora atretica *a* are discussed below).

Another form of atresia occurs when a follicle behaves

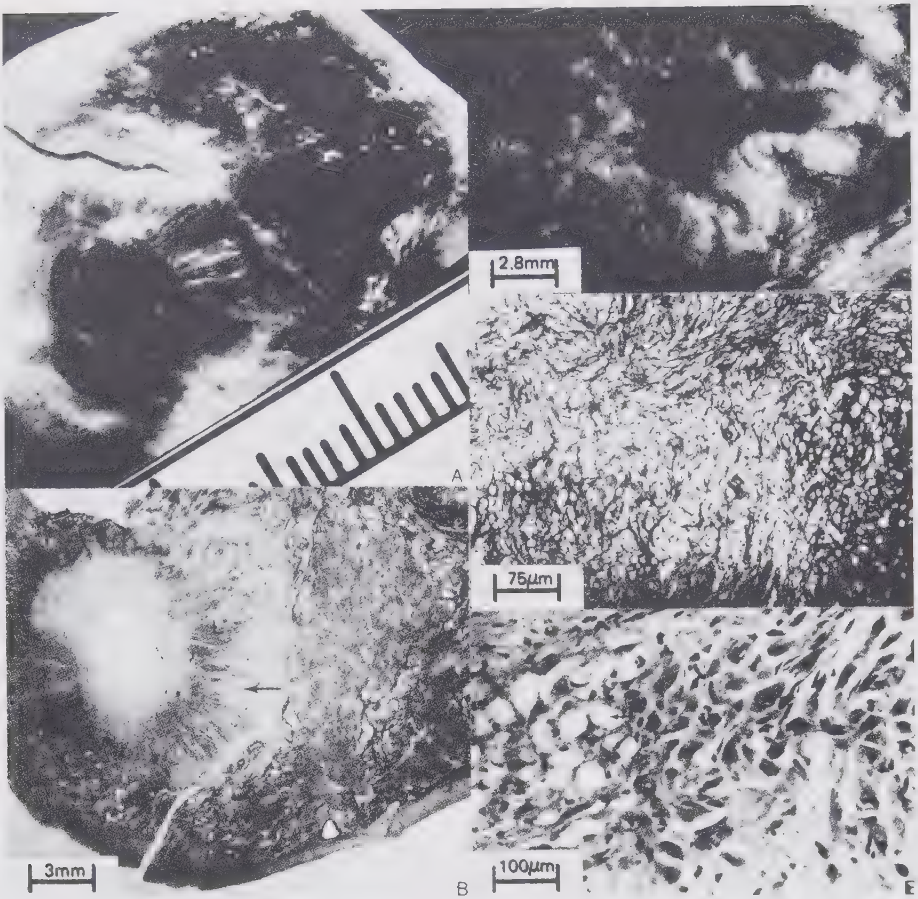

Fig. 2. Structures observed in the ovaries from minke whales, *Balaenoptera bonaerensis*, brought to the workshop by C. Lockyer. The scale is in mm.

A. Macrophotograph of a young corpus atreticum *a* (lower left) and a corpus albicans (upper right). The young corpus atreticum *a* had a fibrin-filled centre and a prominent stigma on the ovary surface.

B. Histological section of the structures in A. The granulosa layer of the corpus atreticum *a* (left side) has been replaced by fibrous tissue. The theca layer has luteinized. Some of the theca luteal cells (L) are still active; others (arrowed) are undergoing fatty degeneration. The corpus albicans is on the right. Stained with van Gieson's stain (Curtis, 1905) and celestin blue haemalum.

C. Macro-photo of an older corpus atreticum *a*.

D. Histology of part of the corpus atreticum *a* in C. Some theca cells, all of which have undergone fatty degeneration, are still present (examples arrowed) but there has been extensive fibrous replacement. Stained with van Giesen and celestin blue.

E. Higher-power photograph of the theca layer in B showing the theca lutein cells before (L) and during (arrowed) fatty degeneration. Stained with van Giesen and celestin blue.

as it would have done had ovulation occurred, but the egg is not released, thus forming an accessory corpus luteum (see multiple corpora, below).

Laws (1961) described 'yellow', 'buff-cellular' and 'yellow and white' corpora aberrantia in fin whale ovaries, which he included in counts of corpora albicantia. Gambell (1968; 1972) also recorded corpora aberrantia in sei and sperm whales respectively and included them in corpora counts. Similar structures were also observed in sperm whale ovaries by Chuzhakina (1963). Best (1967) described similar bodies, also in the sperm whale, which he called corpora atretica *a*, excluding them from his counts of corpora albicantia. Marsh and Kasuya (this volume), observed these structures in *Globicephala macrorhynchus* ovaries, followed Best's terminology and did not include them in corpus counts.

These structures can be derived from ruptured follicles in which corpus luteum development has not proceeded normally (Best, 1967). As these bodies seem to result from mainly thecal luteinization (like the smaller corpora atretica *b* described above), Best (1967) suggested that these structures should be called corpora atretica *a*.

The term 'corpora aberrantia' should be avoided, as it has a different and precise meaning in the general ovarian literature (see Harrison and Weir, 1977).

Fig. 2A shows the general morphology of a young corpus atreticum *a*. The granulosa layer has been replaced by fibrous tissue. Extensive thecal luteinization has occurred on one side of this body. Some of the thecal lutein cells still appear active, others are undergoing fatty degeneration (Figs 2B, E). A fibrin clot fills the centre. Even though a conspicuous stigma was visible on its surface, this corpus atreticum *a* is macroscopically and histologically quite different from a normal corpus albicans (Figs 2A, B).

Figs 2C, D shows an older corpus atreticum *a* which also appeared to have developed from a ruptured follicle. In this case, a central fibrous clot probably did not develop. The number of lipid-rich luteal cells has been greatly reduced and the fibrous replacement is much more extensive. This structure (Figs 2C, D) is also macroscopically and histologically quite distinct from a corpus albicans. However, it is possible that an old corpus atreticum *a* in which fibrous replacement has been extensive could not be distinguished from a regressing corpus albicans (Laws, 1961; Best, 1967).

Miller and Campbell (1978) discussed cystic corpora lutea in cattle. Such cysts are considered non-pathological and perhaps normal if less than 10 mm in diameter. Like corpora atretica *a* these cysts are formed after ovulation and result from rapid infiltration by fibroblasts through the granulosa layer of the ruptured follicle. Factors which may predispose to this condition include explosive rupture of the follicle, premature closure of the ovulation point and an over-ripe follicle with the membrane propria degenerating at the time of ovulation. Cetacean corpora atretica *a* may have a similar etiology.

As outlined above, the inclusion or exclusion of corpora atretica *a* in counts of normal corpora albicantia is variable with author and results in differences in the interpretation of the ovulation rate and the record of possible past pregnancies. It is proposed that, whenever possible, workers distinguish between the different types of corpora (which may be difficult without histological evidence) bearing in mind that ovulation which is not followed by normal corpus luteum development almost certainly does not give rise to pregnancy.

(4) Corpus luteum

The corpus luteum is the endocrine gland which normally develops from the cellular components of the ovarian follicle after ovulation (Harrison and Weir, 1977). When a foetus is found in the uterus, the corpus luteum is generally referred to as a corpus luteum of pregnancy or a corpus gravidatum. A corpus luteum which persists for a short time without a subsequent pregnancy is termed a corpus luteum of ovulation or a corpus luteum of the cycle.

On morphological grounds cetacean corpora lutea have been classified as everted, cavitate, meandrine, vesicular and non-vesicular (see Laws, 1961). Despite the earlier claims (e.g. Robins, 1954) and the fact that in at least several species most presumed corpora lutea of ovulation are smaller than those accompanying a definite pregnancy (Mackintosh and Wheeler, 1929; van Lennep, 1950; Robins, 1954; Laws, 1961; Sergeant, 1962; Best, 1967; Marsh and Kasuya, this volume), it seems unlikely that the corpus luteum of early pregnancy can be distinguished with certainty from one from a non-pregnant animal (Benirschke, Johnson and Benirschke, 1980).

Several workers including Harrison (1949), van Lennep (1950), Best (1967), Hirose, Kasuya, Kazihara and Nishiwaki (1970), Mossman and Duke (1973), Harrison *et al.* (1981) and Marsh and Kasuya (this volume), have observed two distinct types of gland cells in the corpora lutea of various cetaceans. These have sometimes been referred to as theca and granulosa lutein cells but, as Harrison (1949) pointed out, this classification cannot be verified without following the development of corpora lutea through several stages.

The corpus luteum persists throughout pregnancy in all cetaceans studied. There is also histological evidence that the activity of the corpus luteum changes during pregnancy, in at least some species (e.g. blue and fin whales (Mackintosh and Wheeler, 1929); sperm whales (Chuzhakina, 1963); *Phocena phocena* (Fisher and Harrison, 1970); *Stenella graffmani* [= *S. attenuata*] (Harrison *et al.*, 1972); *Globicephala macrorhynchus* (Marsh and Kasuya, this volume).

(5) *Multiple corpora lutea*

Pregnant cetaceans have been described with more than one active corpus luteum but only one foetus. This phenomenon is very rare in most species (Chittleborough, 1954; Laws, 1961; Sergeant, 1962; Ohsumi, 1965; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), exceptions being the white whale (Brodie, 1972; Sergeant, 1973) and the narwhal (K. Hay, pers. comm., 1981). The relative functions of members of a set of multiple corpora lutea have not been studied. If they differ in size, all but the largest are called accessory corpora lutea. Strictly speaking, the term accessory corpus luteum should not be so limited. In the general mammalian literature, it is applied to any unruptured follicle which forms a corpus luteum irrespective of whether the female is pregnant, (Harrison and Weir, 1977). (See also Laws, 1961; Best, 1967; Marsh and Kasuya, this volume.)

(6) Corpus albicans

Regressing and regressed corpora lutea are now almost always referred to as corpora albicantia whether they are pigmented or not. Even though regression is essentially a continuous process, various cetologists have divided corpora albicantia into several categories to analyse the course of regression (e.g. Laws, 1958, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Larsen, this volume; Marsh and Kasuya, this volume).

Several workers have separated the corpora albicantia observed in various cetaceans into two types (usually on histological grounds) and have suggested that one type might have developed from corpora lutea of ovulation, the other from corpora lutea of pregnancy (e.g. Peters, 1939; Sleptsov, 1940; van Lennep, 1950; Robins, 1954; Zemskiy, 1956; Ivashin, 1958; Hirose *et al.*, 1970; Fisher and Harrison, 1970; Zimushko, 1970; Harrison and Brownell, 1971; Harrison, Boice and Brownell, 1969; Harrison *et al.*, 1972; Collet and Harrison, 1981). The essential distinguishing feature of the two types is usually the amount of amorphous, relatively acellular, hyaline material present. The validity of this distinction has never been confirmed. Most workers who have studied the corpora albicantia from a large series of conspecifics (e.g.

Laws, 1961; Sergeant, 1962; Best, 1967; Gambell, 1968, 1972; Kasuya, 1972; Kasuya *et al.*, 1974; Perrin *et al.*, 1976; Harrison *et al.*, 1981; Marsh and Kasuya, this volume), have not managed to separate corpora albicantia of pregnancy from those of ovulation.

(7) Terms used to describe female reproductive status

(*a*) *Immature*: The female has no corpora lutea or corpora albiantia on her ovaries.

(*b*) *Pregnant*: The female has a live embryo/foetus in her uterus.

(*c*) *Lactating*: The female has active mammary glands producing milk. Some simultaneously pregnant and lactating females have been observed in most cetaceans for which a large series has been studied. These animals should be considered as pregnant in estimating the average length of the reproductive cycle.

(*d*) *Resting*: The (mature) female is neither pregnant nor lactating. As pointed out by Perrin *et al.*, 1977, this is a catch-all phrase which includes females truly resting, i.e. not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to the death of the suckling calf.

(*e*) *Post-reproductive/senescent*: The female either cannot conceive or cannot sustain a pregnancy successfully because of age-related changes to her reproductive system. Marsh and Kasuya (this volume) present evidence for a post-reproductive or senescent phase in the ovaries of *Globicephala macrorhynchus* in which there appars to be no evidence of ovulation after age 40, when females have a life expectancy of 13 years. However, post-reproductive *G. macrorhynchus* are not infrequently lactating. Sergeant (1962) also observed a small percentage of such females in *G. melaena* as did Perrin *et al.* (1976) in *Stenella attenuata* and Perrin *et al.* (1977) in *S. longirostris*. As discussed by Marsh and Kasuya (this volume), it is difficult to be certain that an individual female is post-reproductive.

(*f*) *Post-partum and post-lactation oestrus*: Problems arise in the precise definition of such terms. The shortest times a female can recycle after parturition, cessation of lactation or indeed after unsuccessful oestrus and ovulation are not known for most cetaceans and are likely to be highly variable with individuals both in and between species. The incidence of such events is likely to be more significant in some species than others. It is proposed therefore that these terms be avoided unless specific evidence of timing can be referred to, such as in closely-observed captive animals, or animals where past reproductive history is clear from examination of the entire reproductive tract.

Appendix C

SPECIMEN COLLECTION, PRESERVATION, STORAGE AND PREPARATION

The collection and subsequent examination of cetacean reproductive material is an essential part of the documentation of the species' life history parameters which, in turn, are an essential component of population models. Collection of reproductive material must be accompanied by the collection of earplugs, bullae or teeth for age estimation. The nature and extent of specimen collection will vary greatly with the conditions under which the work is done (e.g. single specimens, mass strandings, drive fisheries, factory ships or incidental kills in other fisheries), personnel available, facilities, etc. The following section is intended to serve as a guide and not as a final determination as to how the work should be done. Each investigator must select the protocol most appropriate for the specific needs of the research project. In addition, new and better techniques will become available from time to time.

(1) *Collection*

The size of the animal and its components will have a great effect on the material collected.

(*a*) *Females*. For small ondotocetes, wherever possible, the entire reproductive tract should be collected and should include the complete vagina (this is obviously impractical for large whales). This technique preserves tissue orientation and lessens the chance of mis-labelling ovaries and the loss of small embryos and vaginal mucous plugs. The flat width of each uterine horn should be taken at the mid-point of each horn. If the animal is obviously pregnant the foetus can be removed and the horn subsequently measured. The ovaries and foetus may be weighed fresh, and it is important that this be noted for subsequent analyses. A detailed comparison of fresh versus preserved weights has not been made. A section of each uterine horn (and vagina) should be taken if the entire tract is not collected.

The mammary glands should be examined and a tissue sample taken. Length, width and thickness of the glands can be measured, but this is often impractical. If thickness is measured, it should be at the thickest part of the gland or a fixed distance from a topographical landmark. The colour of the freshly cut gland should be noted, using a consistent scale (e.g. pink, pink-brown, brown). A milk sample should be collected when possible for nutritional, pollutant and parasitic examination. Ideally, the milk should be taken directly from the teat to avoid contamination. Alternatively it can be taken from the incised reservoir. The colour of the uncontaminated milk should be noted.

Vaginal smears may be taken from fresh animals. Results may vary with the location within the vagina from which the smear is taken. Collections should be from a consistent location or the specific location noted.[11]

(*b*) *Males*. The testes should be weighed and measured (length, width, and thickness when laying flat). In some smaller cetaceans, the testes can be taken intact, while in most cases only samples can be taken. It is important to note whether the testes were measured or weighed fresh or preserved, and with or without the epididymis. If only one testis is taken, it should be so noted and taken consistently from the left or right side.

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[11] Editors' note. In captive bottlenose dolphins, contents of vaginal smears were not correlated with ovulation, but copulation could be confirmed by presence of sperm (V. L. Kirby, pers. comm.).

Samples of the testes should be taken at mid-length and include the core from small whales and both core and peripheral samples from large whales, to account for differential maturation. Epididymis samples can be taken at mid-length, but more sperm are likely to be encountered in the cauda (posterior) epididymis. The testes of most species have not been sampled to determine if there are areas of differential maturation. In any event, sampling sites should be noted and consistent. Smears can be taken from both the cut surfaces of the testes and the epididymis.

The activity of a testis can be determined most accurately through histology, but in general there also appears to be a good correlation between sperm production and the weight of the testis. Histologically, an active or recrudescent testis is characterized by the presence of meiosis and mitosis. This can be easily determined through a 'touch preparation,' in which a few tubules are teased out and touched to a slide. The specimen is then fixed in ether alcohol, stained with haemotoxylin and eosin and examined for very dark cells indicative of meiosis. When a testis is actively producing sperm, the cellular associations characteristic of spermiogenesis (spermatogonia through spermatozoa) can be observed in histological sections and sperm can be seen in smears or teased preparations.

In some terrestrial mammals (e.g. lemurs) testis size can change dramatically with season, but some spermatazoa may be present even when the testes are considered inactive; sperm can remain in the tubules for a long time after initial production, but generally they are not of the same quality as more recently produced sperm.

(2) *Preservation*

(*a*) *Fixatives*. The most widely used fixative is 10% neutral buffered formalin (NBF) or 10% sea-water formalin. Bouin's solution is the traditional fixative for embryological material and may be used for other specimens. Problems arise, however, in the identification of gross structures because of yellow staining by the fixative. A further problem with Bouin's solution is its relatively low power of penetration of tissues. Material fixed in formalin can be refixed in Bouin's (or other fixative) at a later time. Electron microscope (EM) material usually requires fixation in glutaraldehyde, but this is not usually practical when large numbers of animals are being processed. Specimens should be fixed within minutes of death for the best EM results.

Tissue samples should be on the order of one cubic centimetre, to permit rapid permeation of the specimen. Tissue-to-fixative volumes should be on the order of 1:10. Smaller volumes can be used if the fixative can be changed one or more times and the samples agitated. Tissue samples can be individually placed in perforated plastic tissue containers and remain there through most histological processing. Perforated plastic bags can be used to store all samples from one individual. Samples from several animals can be placed in a large container of fixative.

Gross specimens (e.g. large whale ovaries and whole testes) should be slit once longitudinally to ensure fixative penetration. Uterine horns can be injected with 10% NBF.

Containers holding several specimens should be agitated to ensure the samples are not packed together and thus retarding fixation.

Alternative preservation methods include freezing and packing in dry-salt, although these will usually not yield adequate histological preparations.

Milk samples should be preserved by freezing. Formalin can be used if nutritional analyses are not done.

Smears can be adequately preserved by air drying. Specific spray fixatives are available.

(*b*) *Storage*. Formalin-preserved material can be stored indefinitely in tightly sealed containers kept in the dark, although storage for years may affect the quality of histological preparations due to hardening of the tissue. Some routine curation is necessary to prevent samples from being damaged from fluid loss. Addition of 59% (by vol.) glycerine can temporarily prevent specimen damage if fluid is lost.

Smears can be stored in slide boxes, without further attention until stained.

Five-percent (5%) formalin is adequate for the storage of thoroughly fixed material. Likewise, the tissue-to-fluid volume ratio can be reduced to about 1:5. Recent concern has been expressed, however, over the health and safety aspects of the use of formalin, which may be banned from usage in certain laboratories. Concensus was that once fixed in 10% NB formalin, specimens may be transferred to other less noxious preservatives for personnel safety. Alcohol was considered a possible alternative for some tissues, although tissue shrinkage might be a problem.

The use of heat-sealed plastic bags appears to be a superior method for long-term storage. A bag is constructed by heat-sealing one end of a piece of 'Lay flat' plastic tubing; the specimen, preservative and label are inserted, and the bag sealed. A second label can be sealed dry in an adjacent compartment. It is important that nonpermeable (polyester) plastic tubing be used.

Frozen samples can, of course, be stored in the frozen state. Containers should be tightly sealed to prevent oxidation ('freezer burn') and drying.

Samples for EM work must be removed from the fixative after about 24 hours and then stored in a buffer solution until further processing.

(3) *Preparation*

Samples for histological examination are usually embedded in paraffin and stained with hematoxylin and eosin (H & E) after sectioning. Other stains (trichromes) are a matter of individual preference. H & E is the choice of pathologists, as it allows for structure identification in poorly preserved or autolyzed samples. Smears can be stained appropriately and a cover-slip mounting medium applied.

Prior to cutting an intact specimen (especially ovaries), it should be photographed in more than one plane. The resulting working prints may then be used to document the location(s) of any part sliced and subsequently removed for histological examination. Further photographs of cut surfaces, particularly of ovaries, prior to the dehydration and embedding process are also useful; it is often the case that an impression gained macroscopically is different from the final histological picture. Photos should include a scale and relevant identification numbers.

Ovaries have been sliced (in order to count corpora) at varying thicknesses. Certainly thinner slices are necessary for small cetacean ovaries than for large cetaceans, where 2–5-mm is adequate, given the relative sizes of the structures. Sections should be left attached along one side of the ovary where possible, to preserve sequence and orientation. If sections are cut too thin, they will not lay flat during embedding if a complete histological section is subsequently required.

It is important to save ovaries and any other material that may require re-examination and/or reinterpretation. It is impossible to corroborate an interpretation if the material has been discarded.

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Growth and Reproductive Rates in Two Populations of Spinner Dolphins, *Stenella longirostris*, with Different Histories of Exploitation[1]

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ABSTRACT

A model of density-dependent change in net reproductive rate (births minus deaths) has been used in assessing status of dolphin stocks in the eastern tropical Pacific. The eastern spinner population has been estimated to be at a lower fraction of original size (17–25%) than is the population of whitebelly spinners (58–72%). Higher reproductive rates would be expected in the former than in the latter on the basis of the density-dependent model, provided the latter is above its level of maximum net production. Based on analyses of over 4,000 specimens collected through 1978: (1) there is a relative paucity of fully adult males in the eastern spinner population (possibly resulting in lower average fertility), (2) the eastern spinner female attains sexual maturity about one tooth-layer unit (probably one year) earlier than does the whitebelly spinner, (3) ovulation rate in young females is lower in the eastern spinner population, and (4) the proportion of all females which are sexually mature is lower in the eastern spinner population. Gross annual reproductive rates (proportion female × proportion of females mature × pregnancy rate) are not different in the two populations (about 8–10% in both cases). This comparison does not confirm the hypothesis that a density-dependent increase in gross reproduction occurs in the spinner dolphin.

INTRODUCTION

Tuna seiners operating in the eastern tropical Pacific (ETP) kill dolphins incidentally during fishing operations (Perrin, 1969; Fox, 1978). The incidental kill has reduced the abundance of some geographical forms, by as much as 83% (Smith, 1983). The basic model used in assessing the status of stocks and estimating net production has been based on density-dependent change in gross production, i.e. that reproductive rates go up as density goes down (loc. cit.). Such a change has not been observed in a dolphin population; its use in dolphin assessment and management has been based on observations of populations of terrestrial mammals, pinnipeds and two baleen whales (Fowler, 1981). This paper presents the results of a comparative study of two populations estimated to be at different proportions of their initial sizes, in an attempt to validate the assumption of density-dependent change in reproductive rates.

At least four morphologically differentiated stocks of spinner dolphins, *Stenella longirostris* (Gray, 1828), exist in the eastern tropical Pacific (Perrin, 1975a and b; Perrin, Sloan and Henderson, 1979; and Au, Perryman and Perrin, 1979). The two forms treated in this paper are the ‘eastern spinner dolphin’, which occurs from close to the coast of Mexico and Central America to several hundred kilometers offshore, and the ‘northern whitebelly spinner dolphin’, which is a more high-seas form, found north of the equator and ranging west to about 150° W long. In 1979, the population of eastern spinners was estimated to be 17–25% (central estimate 20%) of its initial size, whereas the population of northern whitebelly spinners was estimated to be 58–72% (central estimate 65%) of initial size (Smith, 1983). In assessment and management of the ETP dolphin stocks, maximum net productivity level (MNPL, in numbers of individuals) has been assumed to occur at population size somewhere between 50 and 80% of initial size (Smith, 1983). If it is assumed that the two rather similar populations had similar reproductive rates prior to exploitation, then from the population-dynamics theory outlined above, the current reproductive rates should be higher in the eastern spinner population than in the whitebelly spinner population, providing that MNPL is below 65% and that the form of the density-dependent response is not strongly curvilinear (see Fowler, 1984, for discussion of the form of the density-dependent response). Alternatively, no detectable difference in the reproductive rates could mean that both populations are below (or above) MNPL, that the form of the response is strongly curvilinear, that the two populations had different rates initially, or that density-dependence may exist but act on some other life history parameter. The purposes of this paper are to present estimates of growth and reproductive parameters for the northern whitebelly spinner, as was done for the eastern spinner (Perrin, Holts and Miller, 1977), and to compare the estimates for the two populations.

MATERIALS AND METHODS

The field program

Most of the data and specimens were collected by NMFS scientific technicians aboard commercial tuna seiners. The collection procedures were the same as previously described for the spotted dolphin, *Stenella attenuata* (Perrin, Coe and Zweifel, 1976). Data were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, 30 in 1975, 48 in 1976, 72 in 1977 and 74 in 1978. Some specimens were also collected by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

In 1971 and early 1972, when the field program was

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[1] An earlier version of this paper was working Document SOPS/79/30 prepared for the Status of Porpoise Stocks Workshop, 27–31 August 1979 at the Southwest Fisheries Center, La Jolla, California, and SWFC Admin. Rep. LJ-79-29 (1979).

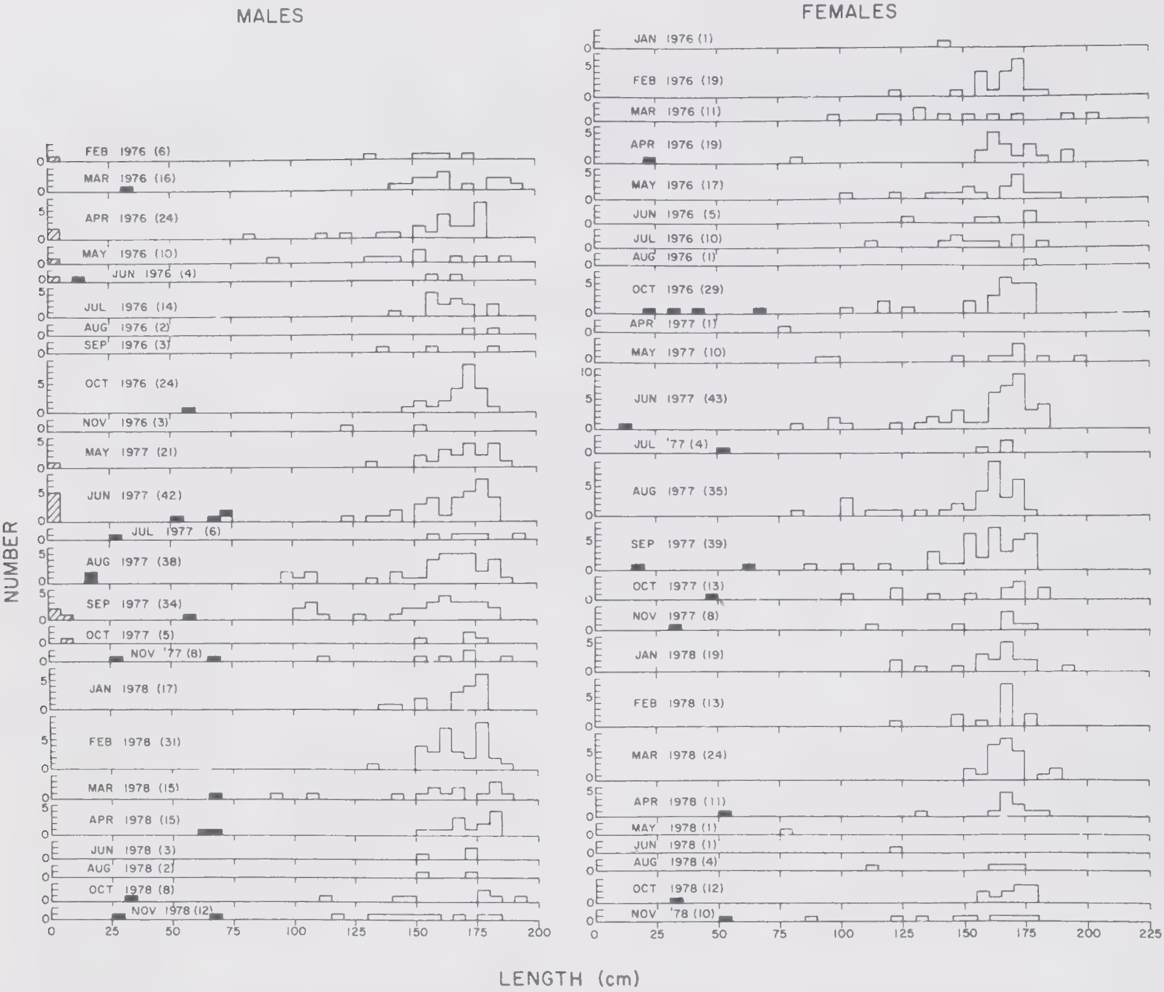

Fig. 1. Length frequency distributions by month and year of eastern spinner dolphins collected 1976–78 and included in the present study. (Sample sizes in parentheses.) Solid squares represent foetuses; hatched squares represent foetuses of undetermined sex (plotted with males).

very limited, adult female specimens were preferentially selected for dissection when available, and the samples for those periods are therefore biased with respect to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was done in determining which animals were to be examined (the attempt was made to examine all the animals in small-kill sets – less than about 30 – and the first 30 or so that came to hand in large-kill sets), and those samples are assumed to be cross-sectional with respect to the kill. Foetuses were not collected in 1968.

The sample of animals for which life history data including, but not limited to, sex and body length were collected includes over 4,000 specimens. Length-frequency data by month and sex were presented for eastern spinner specimens collected before 1976 in Perrin *et al.* (1977); length-frequency data for the balance of the eastern spinner material (1976–78) and the whitebelly spinner specimens are presented in Figs 1 and 2. Charts showing collection localities are presented in Henderson, Perrin and Miller (1980).

The morphological differences between the two races of spinner dolphins are average differences, with considerable overlap, and their geographical ranges overlap, so schools and single-school groups of specimens are identified at sea based on their model characteristics. In case of single specimens or small series of specimens coming from the area of geographical overlap and for which information on the nature of the entire school is minimal, the danger exists of erroneous identification. Such error would tend to obscure any differences between the two populations in reproductive parameters. We were conservative in reviewing identification of such specimens to race, and designated many as 'unidentified spinner dolphins' (excluded from the present study).

Laboratory procedures were the same as reported for the studies of the eastern form of *S. longirostris* (Perrin *et al.*, 1977) and of the spotted dolphin (Perrin *et al.*, 1976).

The NORMSEP computer program was used to define modes in the length-frequency distributions for eastern calves. The program was written by Hasselblad (1966)

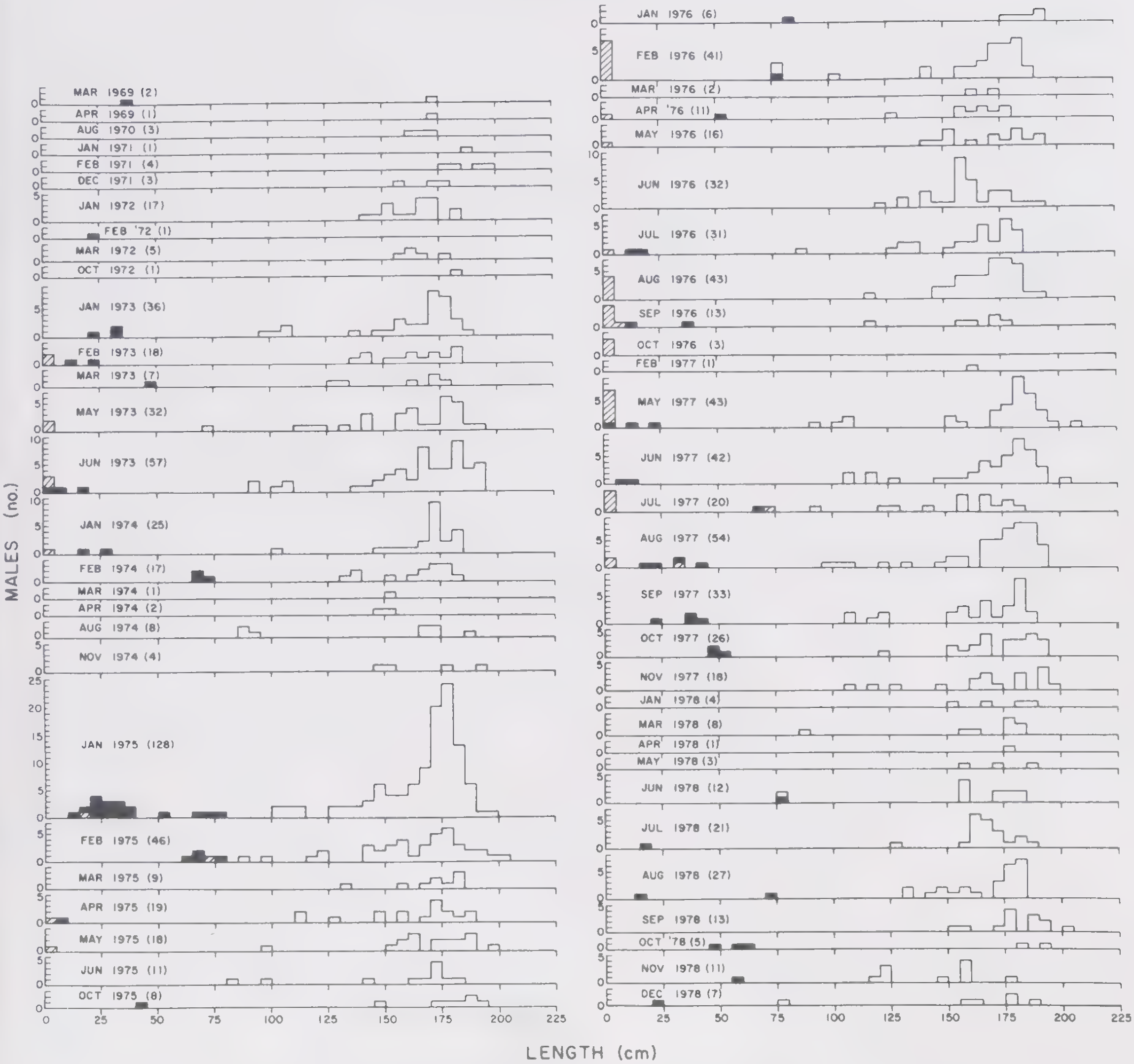

Fig. 2A. Length-frequency distributions by month and year of male northern whitebelly spinner dolphins collected 1969–78 and included in the present study. (Sample sizes in parentheses.)

and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates a mixture of normal length distributions into its components, assuming that the length of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained that would allow estimation of growth rates in juveniles. The computer programs BMDPAR and BMDP3R (Dixon, 1981) were used in fitting nonlinear models.

RESULTS

Growth

Length at Birth

The average length at birth in the eastern spinner was estimated by Perrin *et al.* (1977) at 76.9 cm based on a sample of 101 foetuses and calves, including 23 specimens of the whitebelly spinner and 23 unidentified to race. We estimated average length at birth in the whitebelly spinner based on a sample of 51 foetuses and calves to be 75.9 cm, based on a fit to the logistic model (Fig. 3). We rounded the estimate off to 76 cm in analyses below. The estimate is subject to the same potential biases as that for the eastern spinner (elaborated in Perrin *et al.*, 1977).

Length of gestation and foetal growth rates

We assumed these parameters to be the same in both forms, i.e. 10.6 months and 8.37 cm/month (linear phase), as estimated for the eastern spinner (Perrin *et al.*, 1977).

Postnatal growth

Perrin *et al.* (1977) examined length frequency data for the eastern spinner (data from 1975 and earlier) and found no pattern of length mode progression over time. Growth rates were therefore estimated by more deductive

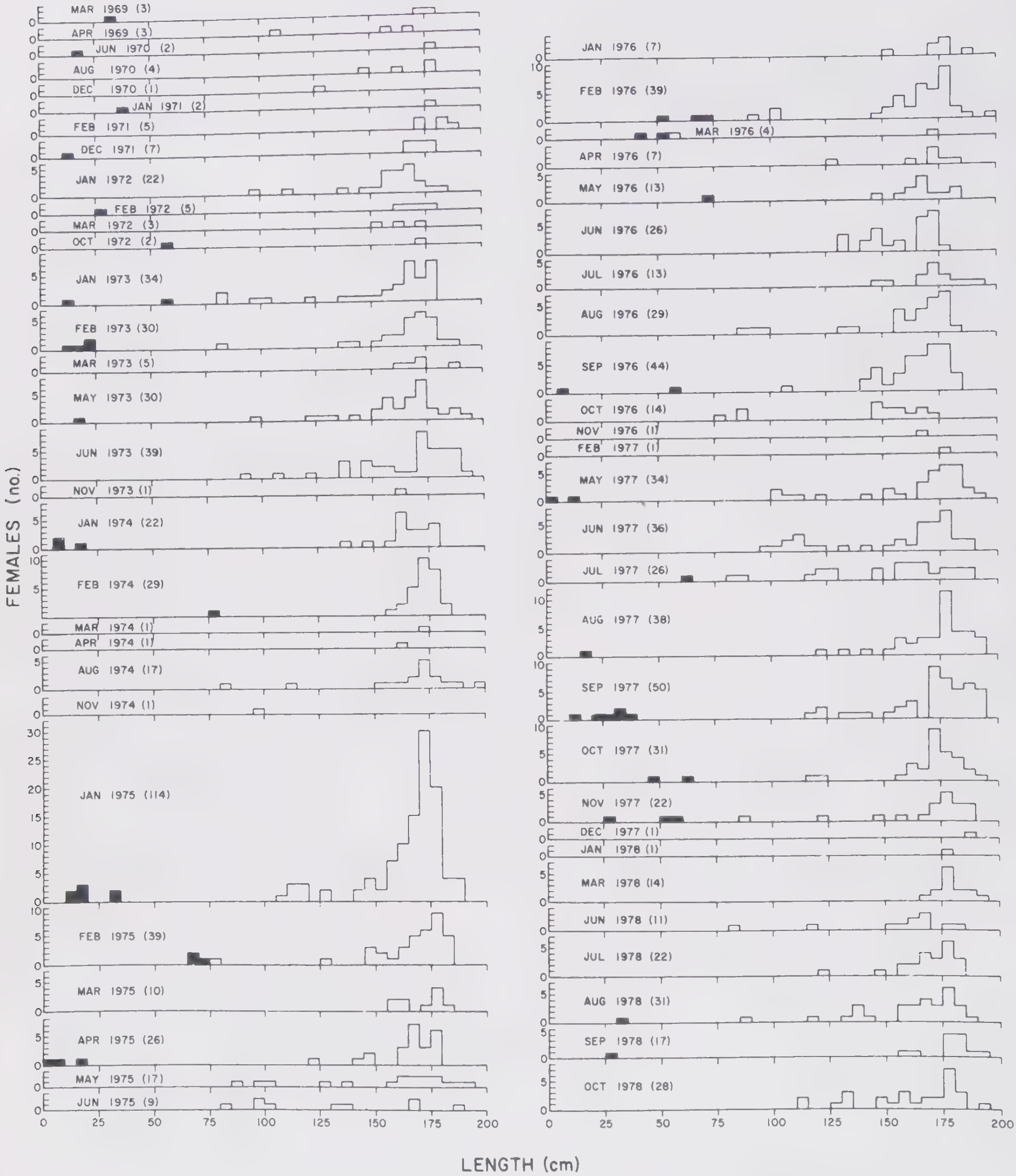

Fig. 2B. Length-frequency distributions by month and year of female northern whitebelly spinner dolphins collected 1969–78 and included in the present study. (Sample sizes in parentheses.)

means. We examined the length frequency data for the whitebelly spinner and encountered a similar situation, i.e. no clear pattern of modal progression with season, this in spite of the finding of seasonal patterns in the birth dates by Barlow (1984). However, re-examination of growth rates in the eastern spinner based on a larger sample than was available for the first study (including data from 1976, 77 and 78) did yield a pattern of modal progression (Fig. 4) covering a span of at least 12 months after birth.

We fit the NORMSEP-estimated modes to the linear model, the logarithmic model and the Gompertz model.

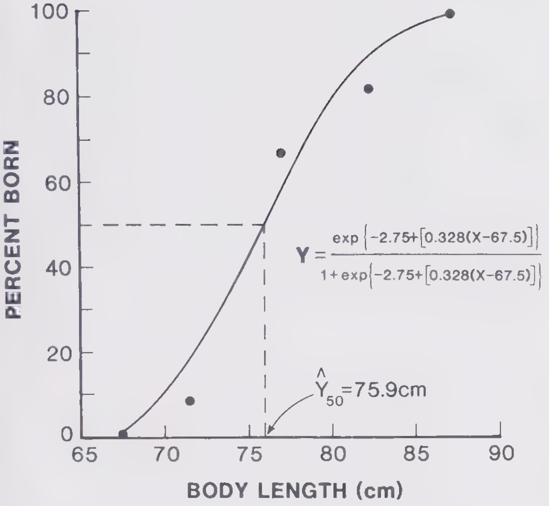

Fig. 3. Estimation of average length at birth, based on least-squares fit of per cent postnatal (percentage that are calves and not foetuses) on body length, in 5-cm increments, to the logistic model for 51 specimens of the northern whitebelly spinner dolphin (24 foetuses and 27 calves) between 65 and 89 cm long.

The Gompertz model provided the best fit (Fig. 3), yielding an estimated average growth rate for the first year of 4.3 cm/month and an average length at one year of 127.5 cm.

Length relative to tooth layering

Perrin *et al.* (1977) presented growth curves and equations for the eastern spinner in terms of length relative to number of postnatal dentinal growth layer groups (GLGs, terminology of Perrin and Myrick, 1980, = 'dentinal layers' in terminology of Perrin *et al.*, 1977). We examined relationships between GLGs and length for 170 male and 232 female northern whitebelly spinners (Fig. 6). The sub-samples for age determination were selected as for the eastern spinner (Perrin *et al.*, 1977).

We fitted curves to the single-GLG means using a two-cycle model[2] as was done for the eastern spinner (loc. cit.), with some differences. (1) The upper end of the second-phase curve (asymptotic length) estimated as it was for the eastern spinner, as the average length of the few very old ($\geqslant$ 13 GLGs) specimens in the samples for both sexes, was lower (by 16 mm in females) than the average length of adult animals, probably a statistical artifact. The procedure resulted in estimates of asymptotic length close to the average sizes of adults (for example 174.9 cm vs 175.2 cm in the females). (2) In the eastern-spinner analysis (Perrin *et al.*, 1977), animals with $\geqslant$ 13 GLGs were pooled into a single class. Whitebelly spinners with $\geqslant$ 15 GLGs were pooled in the final stratum because of a relatively larger number of older specimens – particularly in the male sample. (3) For the eastern spinner, male and female juveniles were considered jointly; the respective length and age means coincided almost exactly. For the northern whitebelly spinner, the

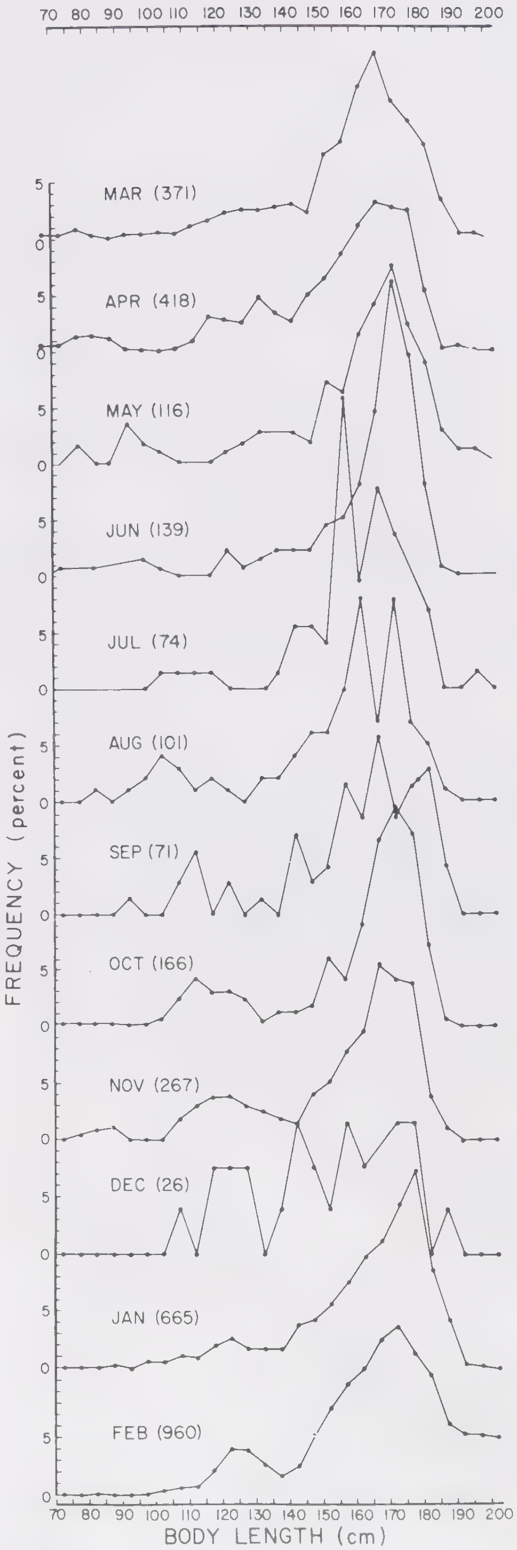

Fig. 4. Length-frequency distributions, by month for all years pooled, of body length in postnatal eastern spinner dolphins. (Sample sizes in parentheses.)

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[2] See Perrin *et al.* (1976) for discussion of the rationale for a two-cycle model.

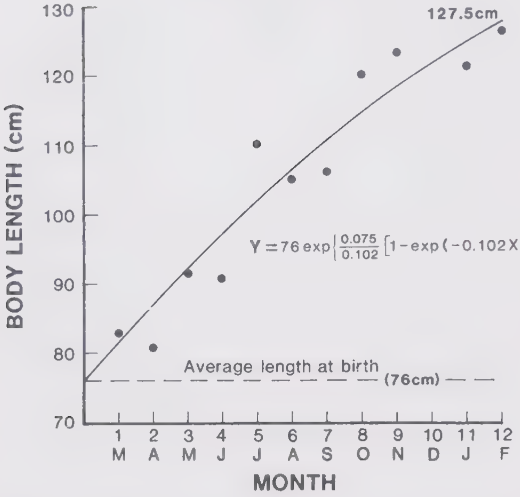

Fig. 5. Least-squares fit to the Gompertz model of mean body-length modes (NORMSEP-estimated from data in Fig. 4) on month of year. December was excluded because of small sample size.

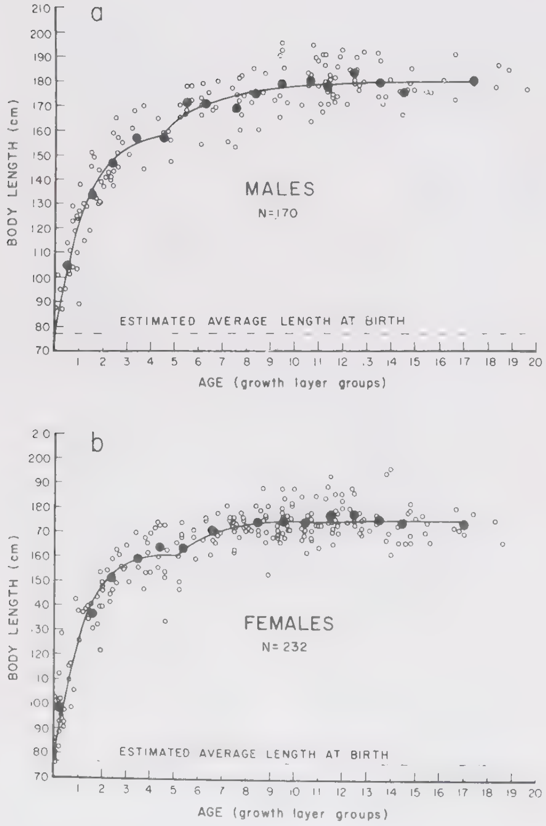

Fig. 6. Relationship between body length and age in northern whitebelly spinner dolphins. Lines are double-Laird-model fits to single-GLG means (solid symbols).

juvenile means differed between sexes, those for the females being higher than those for the males, and the data for juveniles of the two sexes were therefore fitted separately. Age at shift from the juvenile to 'adult' portions of the overall curve (age at onset of the adolescent growth spurt) differed between the sexes. It was 4.4 GLGs in males and 5.1 GLGs in females. Estimated lengths at these ages are 157.8 cm and 160.9 cm, respectively. The shift for the eastern spinner (sexes combined) came at 4.11 GLGs (rounded off to 4 GLGs).

The fitted growth equations for males are, for juveniles < 4.3 GLGs old,

$$L = 77\exp\{0.730[1-\exp(-0.946t)]\}$$

and, for $\geqslant 4.3$ GLGs,

$$L = 157.8\exp\{0.128[1-\exp(-0.480(t-4.339))]\}$$

where L = length in cm and t = age in GLGs.

For females the equations are, for juveniles with < 5.1 GLGs,

$$L = 77\exp\{0.740[1-\exp(-1.117t)]\}$$

and, for age $\geqslant 5.1$ GLGs,

$$L = 160.9\exp\{0.085[1-\exp(-0.775(t-5.145))]\}.$$

The equations rearranged and reduced for estimating age from length are:

♂ < 158 cm

$$t = -1.058\ln(6.954-1.371\ln L)$$

♂ ⩾ 158 cm

$$t = 4.339-2.082\ln(40.542-7.813\ln L)$$

♀ < 161 cm

$$t = -0.895\ln(6.874-1.352\ln L)$$

♀ ⩾ 161 cm

$$t = 5.145-1.292\ln(60.993-11.806\ln L).$$

Length at 1 year of age in the eastern spinner was estimated above at 127.5 cm, based on progression of a length mode. That length is achieved at 1.29 GLGs, from the growth equation in Perrin *et al.* (1977). The previously used estimate of 134 cm (loc. cit.) was deductively derived; corresponding age is 1.57 GLGs, rounded off to the nearest half-GLG to 1.5 GLGs. The new estimate is also close to 1.5 GLGs, and that value is used below for both the eastern and the northern whitebelly spinners. Estimated average length at one year from the growth equations are then 132.5 cm for the eastern spinner and 137.2 cm (average of estimates for males and females) for the northern whitebelly spinner. Lacking a basis for calibrating the growth curve beyond the first year, we provisionally use below three alternative hypotheses for the rate of GLG disposition:

I. One and one-half GLGs per year,

II. One and one-half GLGs in the first year and one per year thereafter, or

III. One and one-half GLGs per year until puberty and one per year thereafter.

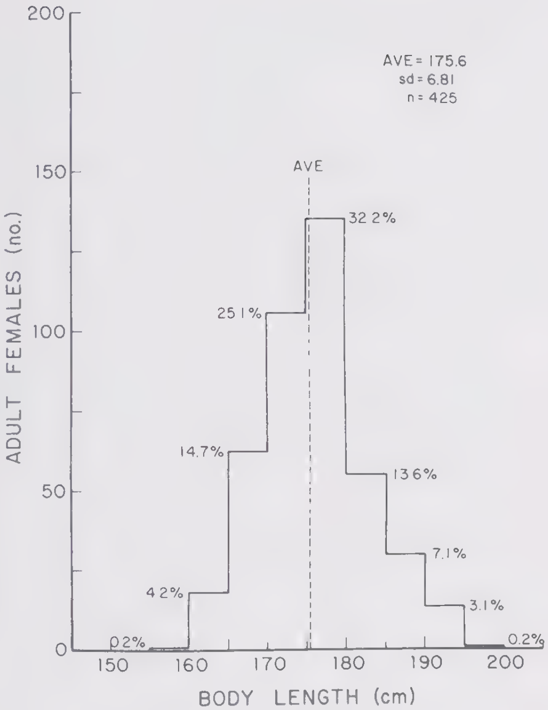

Fig. 7. Distributions of length of sexually adult female northern whitebelly spinner dolphins.

Table 1

Comparison of juvenile growth rates in female eastern and northern whitebelly spinner dolphins

	Average length at 4 GLGs	Average length of adults
Eastern spinner	156.6 cm[1]	171.2 cm ($n = 560$)
Northern whitebelly spinner	159.9 cm	175.6 cm ($n = 425$)
Difference between races	3.3 cm	4.5 cm

[1] From new growth equation based on females included in pooled juvenile sample in Perrin *et al.*, 1977:

$$L = 77 \exp\left\{\frac{0.6521}{0.8984}[-\exp(-0.894)t]\right\}.$$

Adult female northern whitebelly spinners (those of which the ovaries contain at least one corpus of ovulation) average 175.6 cm in length (Fig. 7), compared to 171.2 cm for eastern spinners (Perrin *et al.*, 1977), a difference statistically significant at $P < 0.0001$ (t-test). Length of adult males is more difficult to assess comparatively because of the absence of a clear criterion for attainment of sexual maturity (discussed below in section on male maturation). The difference in length of adult females is reflected in a difference in juvenile growth rates. Size at birth is the same or very nearly the same in the two populations, but juvenile northern whitebelly spinners grow faster than do juvenile eastern spinners, the difference being most pronounced in females (Table 1).

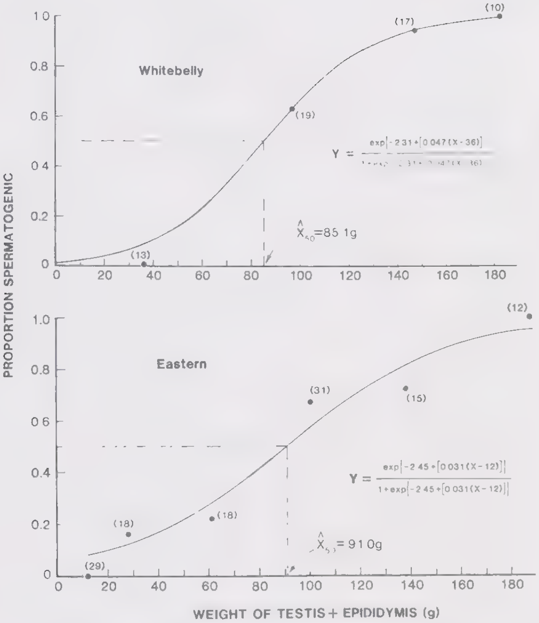

Fig. 8. Least-squares fit to the logistic model of testis-epididymis weight on proportion of males spermatogenic in the northern whitebelly and eastern spinner dolphins. Eastern data from Perrin *et al.*, 1977.

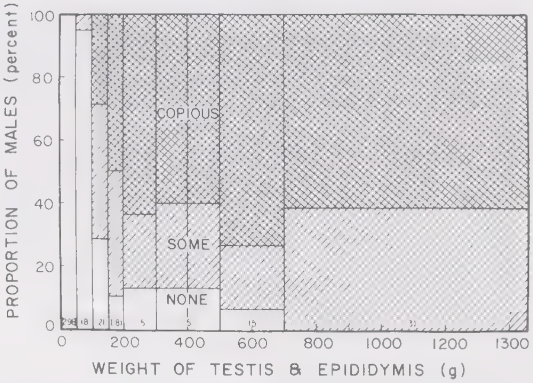

Fig. 9. Amount of sperm in epididymis in relation to combined testis-epididymis weight in northern whitebelly spinner dolphin. Terms defined in Perrin *et al.*, 1976. Sample sizes in parentheses. To be compared with Fig. 18 in Perrin *et al.*, 1977.

Reproduction

The male

There are marked differences between the two populations in morphological indices of reproductive maturity and function for males. Average weight of testis (with epididymis) at onset of spermatogenesis is 85.1 g, based on a logistic fit, in the whitebelly spinner. A similar fit of the data in Fig. 17 of Perrin *et al.*, 1977 for the eastern form yields a 50% value of 91.0 g (Fig. 8B). The two estimates of 91.0 g and 85.1 g are not statistically different from each other. The rounded-off average of 88 g is used below for both forms. The further course of average testicular development differs sharply between

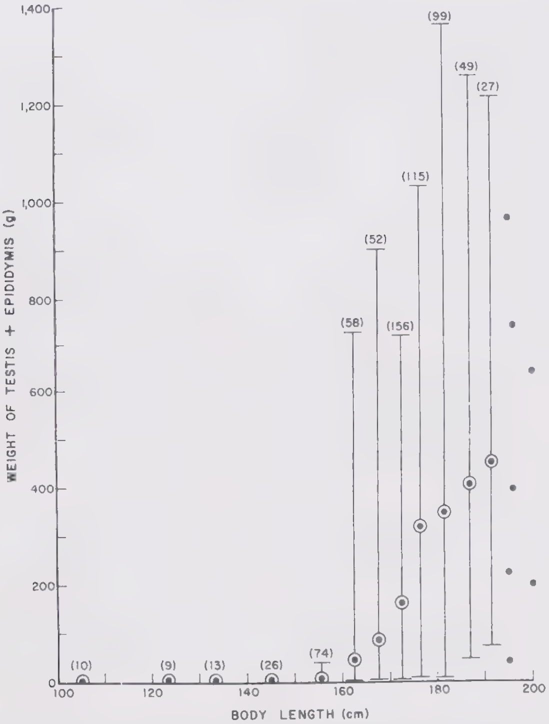

Fig. 10. Relationship between testis-epididymis weight and body length in the northern whitebelly spinner dolphin. Sample sizes in parentheses. Circled dots are sample means; vertical bars are ranges. Dashed circles are means for eastern spinner; sample sizes and ranges in Perrin *et al.* (1977).

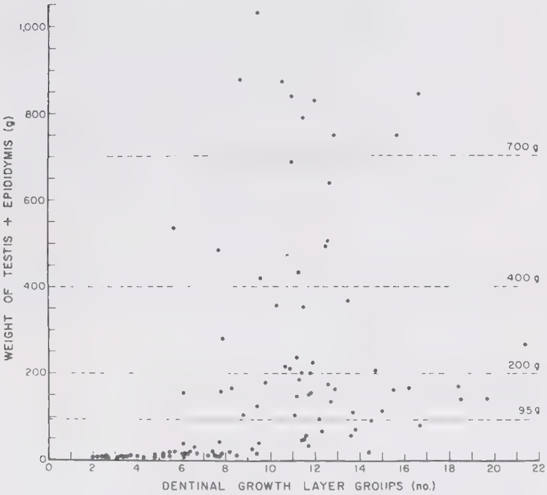

Fig. 11. Scatter plot of testis-epididymis weight on age (in GLGs) for 102 northern whitebelly spinner dolphins.

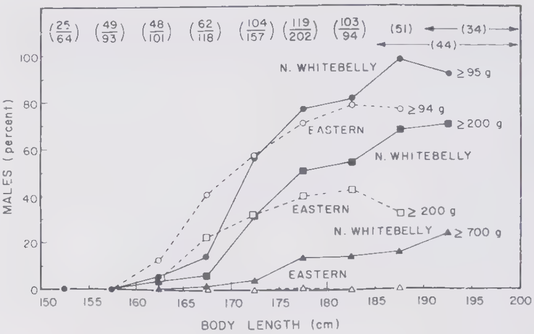

Fig. 12. Proportion of males of given length that have testis-epididymis weights ⩾ 95 g, ⩾ 200 g and ⩾ 700 g in two populations of spinner dolphin: northern whitebelly spinner (solid lines) and eastern spinner (dashed lines). Sample sizes in parentheses (northern – bottom, whitebelly – top).

the two forms. In the eastern spinner, proportion of animals with 'copious' sperm in the epididymis increases to about 50% at testis-epididymis weight of about 400 g (loc. cit.) and levels out, whereas in the northern whitebelly spinner it increases to about 35%, at about 200 g (Fig. 9). In the original eastern sample (Fig. 18 in loc. cit.), no testis weighed more than 700 g, and only a very few of that size (but weighing less than 900 g) have been collected since (unpublished data). However, a sizeable proportion (> 20% at the upper end of body-length size range) of northern whitebelly spinner testes weigh over 700 g (up to 1,354 g in the sample) and all of these examined histologically have had at least 'some' sperm in the epididymis. Amount of sperm in the epididymis would seem to be positively correlated with testis size, and adult eastern spinners have on the average smaller testes than do northern whitebelly spinners of the same length (Fig. 10) (even with a 5-cm adjustment for the racial difference in average length of adults) or age (compare Fig. 11 with Fig. 21 in loc. cit.). At any body length above about 170 cm for eastern spinners and 175 cm for whitebelly spinners, a greater proportion of northern whitebelly spinners attain any particular testis-weight criterion, even the criterion of average weight at first spermatogenesis, and very few eastern spinners attain the high testis weights (> 700 g) associated with 100% incidence of sperm in the epididymis (Fig. 12). At least four alternative explanations suggest themselves: (1) there is seasonal fluctuation in testis size and the differences reflect seasonal biases in sampling, (2) there are inherent differences between the two populations in male reproductive development and morphology, (3) there are differential sampling biases *vis a vis* reproductively active males for the two populations, or (4) testis size (and possibly, male fertility) is depressed in the eastern population, possibly due to some aspect of exploitation.

To address the first of the above possibilities, we examined testis-weight distribution by month for the two populations (Fig. 13). The sample sizes are relatively small for some months, but a clear picture of pronounced seasonality emerges nonetheless. In the northern whitebelly spinner, a mode of large-testis-weight animals appears in February, centered around 700–800 g. The mode persists through May (although possibly retreating slightly), appears in June centered around 400–500 g; moves out to 600–700 g again in July–August; and all but disappears in September through January. The months of peak testis weight (and, presumably, peak fertility and breeding) are February and July–August. The eastern

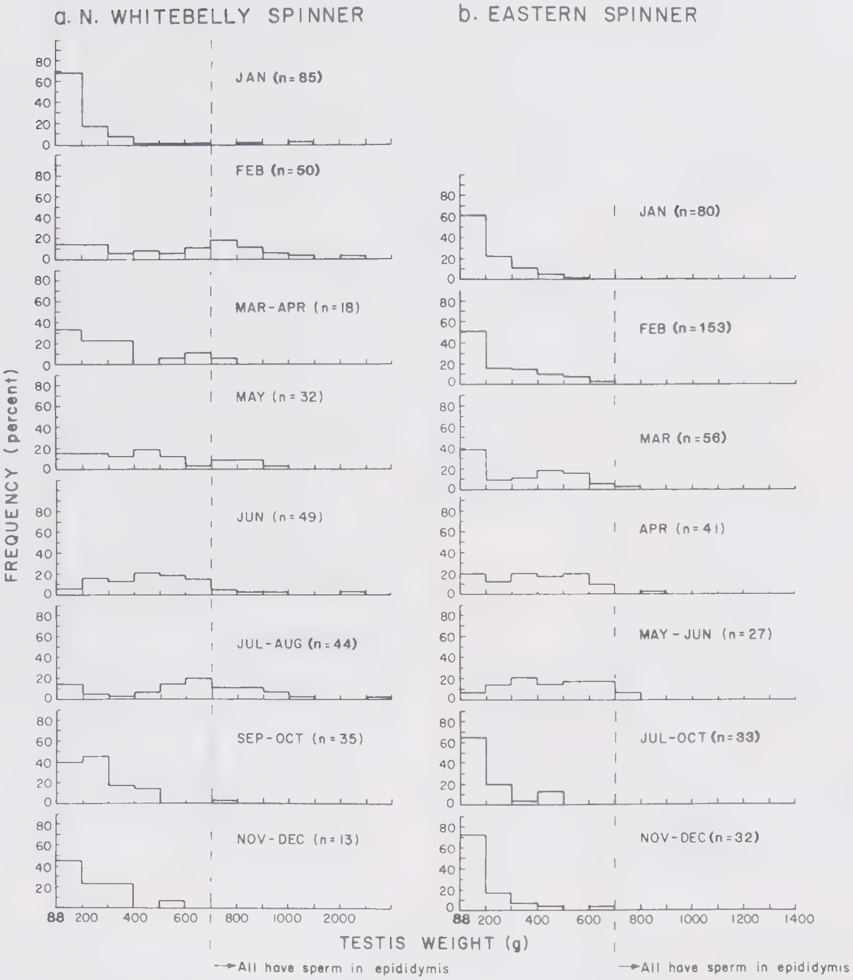

Fig. 13. Testis-epididymis weight distribution by month in two populations of spinner dolphins. Data from 1968–78 (most from 1973–78).

spinner also exhibits seasonality (Fig. 13b), but with important differences. A mode is present in March–June, centered around 400–500 g rather than around 700–800 g as in the northern whitebelly spinner. Only a very small proportion of the animals in the seasonally appearing mode in any month extend above the 700 g level, above which all individuals can be expected to have sperm in the epididymis. The apparent dearth of large-testis males, therefore, in the eastern samples is not an artifact of seasonally biased sampling.

The second alternative, that of inherent difference in testis weight, is unlikely because of the similar testis weight at first spermatogenesis and similar adult body length in the two populations.[3] The third alternative is also unlikely, because fishing practices do not differ with type of spinner dolphin involved. Of the four alternatives considered here, the most likely is that of depression of testis weight in the eastern spinner population, although inherent difference in testis size or differential sampling bias cannot be eliminated from consideration completely.

The female

Attainment of sexual maturity. The smallest sexually mature whitebelly spinner female (possessing at least one corpus of ovulation in the ovaries) encountered was 157 cm long, and the largest immature female was 188 cm long. This compares to 152 cm and 182 cm in the eastern spinner (Perrin *et al.*, 1977). The differences reflect the above-discussed approximately 5-cm difference in average length of adult females. Average length at attainment of

[3] There is one other instance (based on adequate samples and comparable methods) of wide variation in maximum testis weight between populations of a single delphinid, that of *Delphinus delphis* in the Black Sea ($n = 2{,}138$, maximum weight = 1,000 g) and in the eastern North Pacific ($n = 31$, maximum weight = 1,672 g) (Perrin and Reilly, 1984). In this case also, the population with smaller testes is the more exploited one, in fact thought to have crashed because of over-exploitation (Smith, 1982). The difference between average lengths of adults in the two populations may be greater than for the two populations of *S. longirostris*, because the Black Sea form is relatively very small (Perrin, 1983).

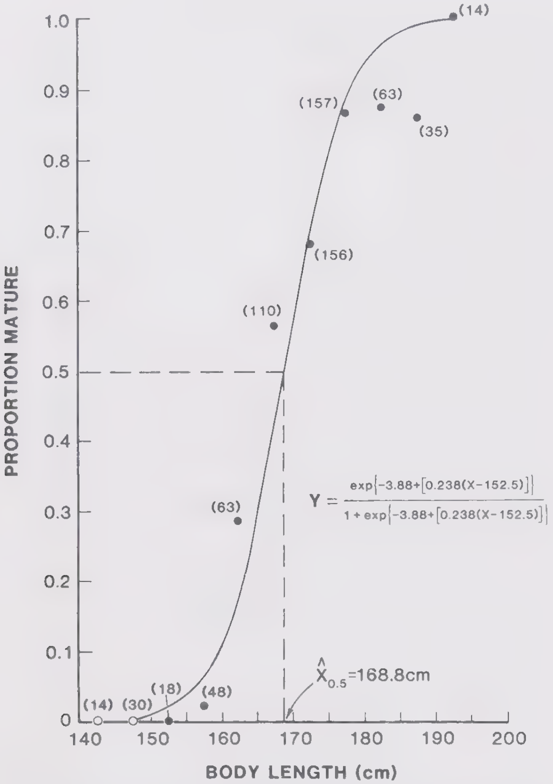

Fig. 14. Estimation of body length at which 50% of female northern spinner dolphins show ovarian evidence of sexual maturity, based on weighted least-squares fit to the logistic model. Sample sizes in parentheses. Open circles not included in regression.

sexual maturity differs between the two populations in the same direction (167.2 cm in the northern whitebelly spinner (Fig. 14) vs 164.1 cm in the eastern spinner (Fig. 22 in loc. cit.). The difference (4.7 cm) yields a younger predicted average maturation age (from the growth equations) in eastern spinners (5.2 GLGs) than in northern whitebelly spinners (7.1 GLGs).

Another estimate of average length at attainment of maturity is that length for which the number of longer immature animals is equal to the number of shorter mature animals. This point for the northern whitebelly spinner is 170 cm and for the eastern spinner is 165 cm, yielding estimates of age at maturation of 6.5 and 5.8 GLGs, respectively. These may be underestimates, because the method does not take mortality into account.

An estimate of length at first conception (not necessarily the same as age at first ovulation) can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Sixteen primiparous northern whitebelly females averaged 171.6 cm in length. Predicted age at that length is 6.95 GLGs. The average length of their fetuses was 248 mm. This length is attained at about 4.3 months. Using the growth equations above to predict growth during 4.3 months for the various tooth-layering models and subtracting the growth increment from 171.6 cm yields estimates of length at first conception ranging from 169.7 cm (6.4 GLGs) to 170.4 cm (6.6 GLGs). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because some females may ovulate several times, and presumably continue to grow, before becoming pregnant the first time. Also, this method

Table 2

Results of analyses of length and age at attainment of sexual maturity in two populations of spinner dolphins. Values calculated with the growth equations are in parentheses

	Length (cm)		GLGs (no.)		Age (years) under hypotheses					
					I		II		III	
Methods (and comments)	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.
1. Length at which 50% have corpora (probable underestimate)	168.8	164.1[1]	(7.1)	(5.2)	4.7	3.5	6.6	4.7	5.3	3.8[5]
2. Length at which mature below equals immature above (possible underestimate)	170.0	160.0[2]	(6.5)	(5.8)	4.3	3.9	6.0	5.3	4.8	4.4
3. Number of GLGs at which 50% have corpora (interpolation, but small sample sizes)	(170.8)	(164.2)	6.7	5.3[1]	4.5	3.5	6.2	4.8	5.0	3.9
4. Length at first conception,[3] under hypothesis:										
I	(169.7)	(–)	(6.4)	(—)	4.3	(—)	—	—	—	—
II	(169.7)	(—)	(6.6)	(—)	—	—	6.1	(—)	—	—
III	(170.4)	(—)	(6.6)	(—)	—	—	—	—	4.9[4]	(—)

[1] From Perrin *et al.* (1977).

[2] Includes data through 1978.

[3] No estimates for the eastern spinner by this method; see text.

[4] Switch from 1.5 to 1.0 GLG/year assumed to occur at 161 cm (5.41 GLGs).

[5] Ditto, at 157 cm (4.13 GLGs).

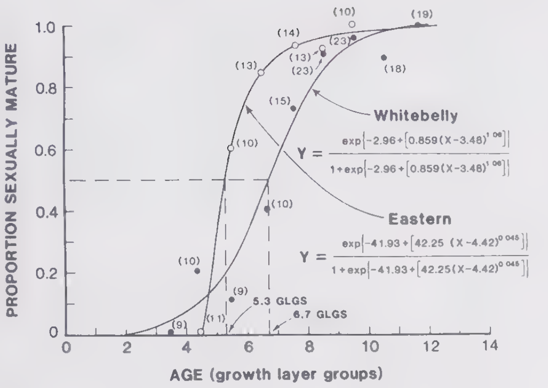

Fig. 15. Relationship between proportion of females sexually mature and age (in GLGs) in two populations of spinner dolphins, based on weighted least-squares fit to a generalized sigmoid model (described in text). Sample sizes in parentheses.

Table 3

Calculation of estimates of gross annual reproductive rates in two populations of spinner dolphins, based on pooled data for 1973–78. Approximate 95% confidence limits are ±2 S.E. Sample sizes in parentheses. From Henderson *et al.*, 1980

	Northern whitebelly spinner	Eastern spinner
A. Percent female	50.9±2.4 (1,778)	51.0±1.8 (2,938)
B. Percentage of females reproductive	52.2±3.6 (905)	43.2±2.8 (1,492)
C. Annual pregnancy rate (percent)	35.6±5.0 (366)	33.9±4.2 (521)
A×B×C. Gross annual reproductive rate (percent)	9.4±1.4 (1,631)	7.5±1.2 (2,624)

assumes no effect of pregnancy on growth rate. Average length of 16 primiparous eastern spinners (171.4 cm) slightly exceeded the estimate of asymptotic size (170.9 cm) used in the growth curve fit; an estimate from the growth equation, therefore, was not possible for the eastern spinner.

Estimates of age at sexual maturity were also derived directly from the smaller samples for which age determinations (GLGs in dentine) were made (Fig. 15), bases on a weighted (weight = inverse of variance estimated as $\mathrm{Var} = p(1-p)/n$) least-squares fit to a generalized sigmoid function:

$$Y = \frac{\exp(a+bX)^c}{1+\exp(a+bX)^c}$$

where a, b and c are fitted parameters. The estimates are 5.3 GLGs in the eastern spinner and 6.7 GLGs in the northern whitebelly spinner. The fitted curves, albeit based on few and small samples, are quite different in form.

The largely independent different estimates of age (in GLGs) at maturation are not widely disparate (Table 3). Averaging of the estimates for the northern whitebelly spinner by the various methods (using Option II in Table 3 of 1 GLG/year after the first year) yields a value of 6.7 GLGs, which value is used below. Averaging of the two relatively most reliable estimates available for the eastern spinner yields an estimate of 5.6 GLGs.

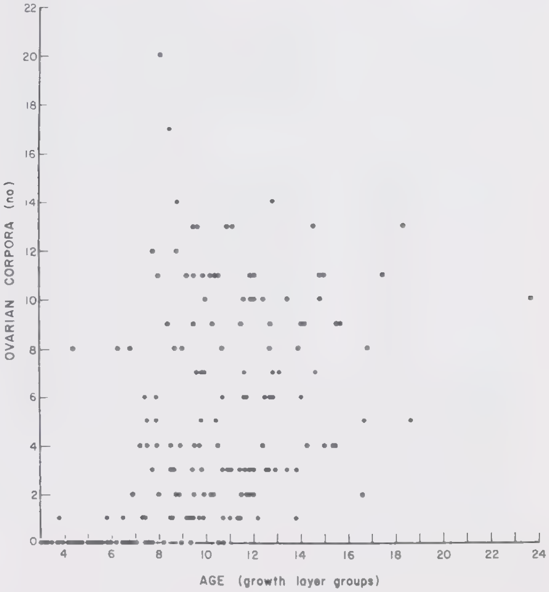

Fig. 16. Scatterplot of number of ovarian corpora on age in GLGs in the northern whitebelly spinner dolphin.

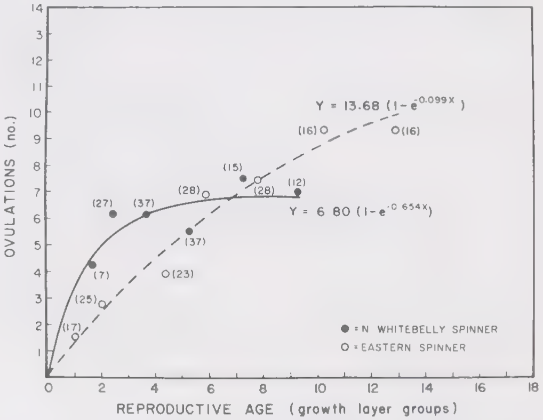

Fig. 17. Asymptotic fit of corpus count on average reproductive age in the northern whitebelly spinner dolphin. Dashed line is asymptotic fit to data for eastern spinner (Fig. 27 in Perrin *et al.*, 1977). Origin set at 0.001/0.001.

If it is assumed that one GLG is deposited after the first year (Hypothesis II in Table 3), female northern whitebelly spinners on the average mature at about 6 years of age and eastern spinners at about 5 years.

Ovulation Rate. Number of corpora in the ovaries (an index of reproductive history of the individual female dolphin) increases sharply at about 6–7 GLGs in the northern whitebelly spinner (Fig. 16) and at about 5–6 GLGs and more rapidly in the eastern spinner (Fig. 6 in Perrin *et al.*, 1977). To estimate ovulation rate, the required estimates of average reproductive ages for 2-GLG intervals were calculated as in Perrin *et al.* (1977).

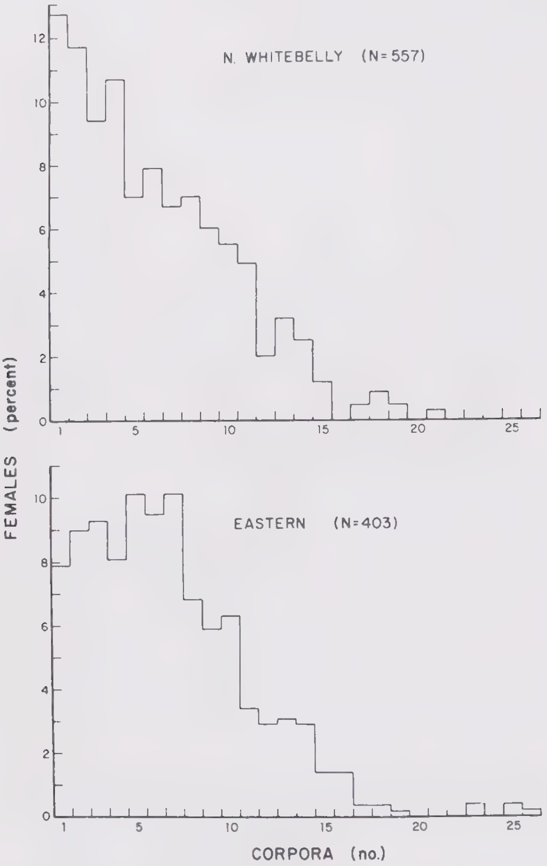

Fig. 18. Frequency distribution of corpus count in two populations of spinner dolphins. Includes samples from 1973–78.

Table 4

Percentage of females sexually immature in two populations of spinner dolphins, 1973–78. Sample sizes in parentheses. From Henderson *et al.*, 1980

Year	Northern whitebelly spinner	Eastern spinner
1973	48.9 (133)	54.4 (344)
1974	40.8 (49)	55.3 (396)
1975	45.5 (191)	57.0 (402)
1976	52.9 (191)	59.4 (106)
1977	48.2 (222)	59.7 (92)
1978	50.0 (118)	70 (92)

Table 5

Summary of parameters for two populations of *Stenella longirostris*. Sources in text and Tables 2–4

Parameters	Eastern spinner	Northern whitebelly spinner
1. Proportion of original population size	17–25%	58–72%
2. Length of gestation	10.6 months (0.88 year)	10.6 months (0.88 year)
3. Average length at birth	77 cm	76 cm
4. Average length at one year (1.5 GLGs, from growth curves)	132.5 cm	Ave. for M & F 137.2 cm
5. Average length of sexually mature female	171.2 cm	175.6 cm
6. Smallest adult female	152 cm	157 cm
7. Largest adult female	182 cm	188 cm
8. Average length of female at attainment of sexual maturity	164.1 cm	167.2 cm
9. Average age at attainment of sexual maturity in female (average of estimates by several methods)	5.6 GLGs (~ 5 years)	6.7 GLGs (~ 6 years)
10. Proportion of population female	0.510	0.509
11. Proportion of females reproductively adult	0.432	0.533
12. Annual pregnancy rate	0.339	0.356
13. Gross annual reproductive rate	0.075	0.094

Ovulation rates were estimated by fitting asymptotic curves to the 2-GLG-interval means of average reproductive age (Fig. 17) (assumes eventual cessation of ovulation in old females). Ovulation rate, as measured by these fits, in young females is higher in the northern whitebelly spinner than in the eastern spinner, but also levels off faster. The relative behavior of the two curves beyond about 8 GLGs of reproductive age may be greatly influenced by the small sample sizes involved at the higher ages, however, and all that can be said with some certainty is that during the first few years of reproductive life spinners in the eastern population ovulate less frequently than do those in the northern whitebelly population.

The shape of the corpora-count frequency distribution is an index of ovulation rate independent of the above fit to the corpora count on reproductive age. The distributions differ in the two populations (Fig. 18), most markedly so between 0 and about 7 corpora. The pattern of difference (higher frequency in the whitebelly population between one and four corpora and the reverse between four and seven corpora) can be explained by initial higher ovulation rate in the northern whitebelly population (although this does not take into account the possibility of differential mortality rates). The results of the two analyses agree quantitatively as well; the asymptotic fits (Fig. 17) estimate that about seven corpora represents about the same reproductive span in the two populations, about seven GLGs (about 7 years, if a one-GLG/year deposition rate is assumed).

Gross production. Gross annual reproductive rate, estimated as proportion of the population female times proportion of females sexually mature (and not post-productive) times annual pregnancy rate (proportion of reproductive females divided by length of gestation – 0.883 year), did not differ between the two populations for the period 1973–78 (Table 4). Overall sex ratio was virtually identical in the two (very large) samples, about 0.96:1. The age structure of females, however, was quite different. Fifty-two percent of the northern whitebelly females were sexually mature, whereas only 43% of the eastern females were mature. The difference is statistically significant at α 0.05 (*t* test). (A larger proportion of females were immature in the eastern than in the northern whitebelly samples for each year, 1973–78 (Table 5).) Pregnancy rate was about the same in the two populations, perhaps reflecting the above-discussed earlier age at maturity. The estimate of gross production was slightly higher for the northern whitebelly population than for the eastern population. The difference, however, is not statistically significant at $\alpha = 0.05$[3].[4]

DISCUSSION

Although differences exist between the northern whitebelly spinner and eastern spinner populations in several growth and reproductive parameters (summarized in Table 5), there is no clear basis for inferring that historically greater exploitation of the eastern spinner has resulted in a higher gross reproductive rate for the population. As would be expected, age at attainment of sexual maturity is lower in the eastern spinner population, but the major difference between the two populations in terms of gross production is in the proportion of females that are sexually mature. Although eastern specimens mature earlier, the mortality rate in this population may be sufficiently greater to effect a reproductively significant downward shift in age structure. In addition, the dearth of mature males hardly seems an adaptive population response and conceivably is an effect on male maturation structure (and perhaps age structure) by the purse-seining operation, through age- and maturity-selective fishing mortality, disruption of maturity-inducing social structure, or some other mechanism. In short, density-dependent population response in reproductive rates induced by the fishery may be counteracted by a more direct effect of the same fishery.

The various parameter estimates used here may be subject to sampling bias of various sorts. The bias in favor of calves in small-kill samples found in the case of the offshore spotted dolphin (Henderson *et al*., 1980) was not found to be significant in the spinner-dolphin samples, although that does not eliminate the possibility of systematic bias in sampling from kills of all sizes. In any case, it can reasonably be assumed that whatever sampling biases exist are operating similarly for samples from the two populations. A possible exception to this is seasonal bias, as both reproduction and sampling are differentially seasonal (Barlow, 1984), but the effect, if any, can be presumed to be very small because of the length of gestation (almost a year) and the relatively diffuse nature of the reproductive seasonality.

As noted above, one alternative hypothesis to that of non-response (in reproductive rates) to exploitation in the eastern spinner population is that response has occurred in both populations, i.e. that the northern whitebelly spinner population even at 58–72% of its original size is substantially below its level of maximum productivity. In this context it would be useful to examine reproductive rates in a third population, the southern whitebelly spinner population, which has been more lightly exploited than the other two (Smith, 1979, 1983). Sample sizes to date have not been large enough to allow meaningful comparisons (Henderson *et al*., 1980), although the trend in pregnancy rates with status for the three populations (higher rate with heavier exploitation) is consistent with the hypothesis that the northern whitebelly population has already responded to exploitation (Perrin and Reilly, 1984).

Although it has been assumed in assessment of the dolphin populations that there has been no effect of exploitation on survivorship (Smith, 1979, 1982), the possibility that such an effect exists cannot be ruled out. The possibility can be examined only through analysis of large representative samples of ages. The age analyses carried out in the study reported here were based on selected stratified samples that were aged to allow estimation of an age/growth curve; these aged samples were not adequate to allow estimation of populational age structure.

The results here point out the need for further research on the biology of the several populations, particularly on age structure and on male reproductive functional morphology and physiology.

ACKNOWLEDGEMENTS

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Reproductive Parameters of Dolphins and Small Whales of the Family Delphinidae

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ABSTRACT

The purposes of this review are to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications. Reviewed are gestation period, fetal growth rate, size at birth, size and age at attainment of sexual maturity, average size and age of adults, maximum size, asymptotic length, ovulation rate, pregnancy rate, calving interval, length of lactation, weaning age, length of "resting" period, age and sex structure, and birth rates. Also discussed are the effects on the estimates of seasonality, schooling segregation, geographical variation and exploitation and the relationships between parameters.

INTRODUCTION

Many populations of dolphins and small whales are exploited directly or incidentally (IWC, 1976–83) and must be assessed and managed. Most of the approximately 32 species (Mitchell, 1975) are poorly known, and the published information on them is scattered in a diverse and often obscure literature. For some species the literature contains widely varying estimates of parameters, a matter of some concern when scientists are asked to provide advice for management (e.g. see Smith, 1983).

The purposes of this review are several: to describe and critique methods used to estimate reproductive parameters, to summarize estimates in the literature and to examine patterns in the estimates and their implications.

It is not the purpose of this paper to review reproductive morphology, physiology, behavior or pathology, except to the extent that they are immediately relevant to estimation of parameters used in stock assessment and management. Broad reviews of reproductive morphology and function have been presented by Harrison (1969), Harrison, Brownell and Boice (1972) and others. Other relevant papers are contained in this volume.

METHODS

In assembling parameter estimates we surveyed as much of the literature as was possible under the time constraints for publication of this volume. We do not believe that we have missed any major references and, while some length data may have been missed, the ranges of values presented here should be definitive of the present state of knowledge of the delphinids. We did not include data from the popular or semi-popular literature unless an obviously measured value was specified and the source of the information could be determined. We did not include lengths identified as estimates, but undoubtedly some of the supposed measurements are in fact estimates. We took considerable pains to avoid inclusion of the same data more than once but there likely is some duplication. We have taken into account information in other papers in this volume. However, because of considerations of timing this was not possible in all cases.

Body length can be measured in several ways: from the tip of the upper jaw to the notch in the flukes, or to the posteriormost extension of the flukes; in a straight line, or over the curvature of the body. We've tried to include only linear beak-tip-to-notch lengths, but some of the included lengths were probably taken in other ways, possibly contributing artificially to the range of length.

For derived estimates, such as average length of adults, we have included published estimates or have calculated the estimates ourselves where only raw data were published or for samples pooled across sources. We calculated standard deviations where sample size was adequate (⩾ 25).

Where specific identification was equivocal, we have omitted the data. It is possible that some early strandings of pilot whales in the eastern North Atlantic referred to *Globicephala melaena* were actually of *G. macrorhynchus* (see Duguy, 1968). Although two species of spotted dolphin (*Stenella* spp.) probably exist in the Atlantic (Perrin, Mitchell and van Bree, 1978), we included data only for specimens referred to *S. plagiodon*, because of the uncertain identity of animals referred to other nominal species (*S. frontalis* and *S. attenuata*).

PARAMETERS

Gestation Period and Fetal Growth Rate

Background and estimation methods

Gestation period is one of the least variable reproductive parameters on a within-species basis in delphinids and in mammals in general (Kiltie, 1982). Estimation of the gestation period is important to stock assessment and management because it comprises one segment of the calving interval. Fetal growth rates are important in determining the age of fetuses and in estimation of the length of gestation.

Estimates of gestation period, of some type, exist for 13 of the 32 delphinid species. Data of varying amounts and quality have been available for producing these estimates. Fetal growth rate has been estimated in only some of these cases. At least seven different methods have been employed. We group them here into three major categories: (*a*) direct observational estimates, (*b*) statistical

Table 1

Outline of the methods used to estimate gestation period for small cetaceans, with species for which the methods have been used

	DIRECT	
I.	Live captive	
	Tursiops truncatus	*T. aduncus*
II.	Embryology	
	Orcinus orca	*Lagenorhynchus actus*
	STATISTICAL	
III.	Huggett and Widdas/Laws	
	a. Within-population	
	Stenella attenuata	*Globicephala melaena*
	Sotalia fluviatilis	
	b. Comparative	
	Pseudorca crassidens	*Berardius bairdii*
	Pontoporia blainvillei	
IV.	Sacher and Staffeldt	
	Stenella longirostris	*T. truncatus*
V.	Comparative G vs L_n	
	a. Other delphinids	*S. longirostris*
	b. Human growth curve	*G. melaena*
	OTHER	
VI.	Visual inspection of data	
	L. acutus	*O. orca*
	Delphinus delphis	*S. coeruleoalba*
VII.	Not reported	
	O. orca	*S. attenuata*
	G. melaena	*D. delphis*
	G. macrorhynchus	*L. acutus*
	P. crassidens	*L. obliquidens*
	T. truncatus	

estimates from series of specimens, and (*c*) 'other,' mostly non-rigorous methods (Table 1).

A. Direct observation

Captive animals. Estimates of this type are available for *Tursiops truncatus* only. The dates of conception and birth were observed for tank-held individuals. There are actually only a very few cases where conception date was known, with a larger series of observed births. Similar data may exist for other delphinids, but we did not find them.

Embryology. Guldberg and Nansen (1894) estimated gestation periods for *Orcinus orca* and *Lagenorhynchus acutus.* They gave detailed descriptions of the state of development of 'representative'-sized fetuses with collection dates and then inferred gestation periods qualitatively. This may have been an accurate technique, but Guldberg and Nansen's estimates have not to date been verified by direct observation or by statistical estimates based on data series.

B. Statistical estimates

All estimates in this category utilize standard regression techniques. Most require discrimination between modes in the distribution of fetal sizes by collection dates.

Method of Hugget and Widdas (1951)/Laws (1959). This the most commonly used technique for mammals in general, including delphinids. It utilizes the empirical concept that fetal growth in length (L) or cube root of weight ($W^{\frac{1}{3}}$) is directly related to time, and that two observable phases occur: a linear phase for most of the period, preceeded by a briefer nonlinear phase (Fig. 1).

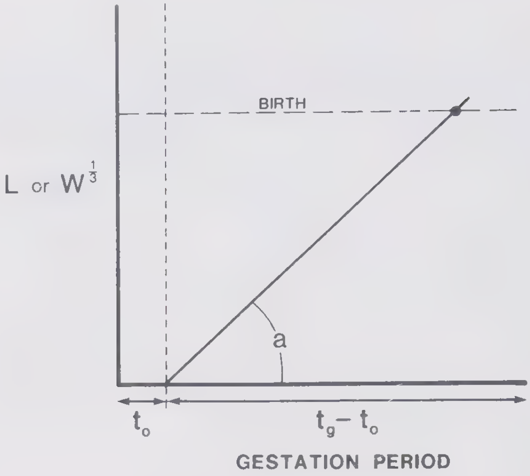

Fig. 1. Estimation of gestation period (t_g) and fetal growth rate (a) by the method of Hugget and Widdas (1951). L is total length, W is body weight, t_0 is the early 'nonlinear' phase of growth.

In estimating the total gestation period the gestation time is divided into two phases. One phase (t_g–t_0) extends to birth from the point where a straight line fitted to the data intersects the time axis. The other phase (t_0) is from conception to the intersection. The linear phase is usually defined by a least-squares fit of time to modal points in L or $W^{\frac{1}{3}}$. The slope of the linear phase a is termed the fetal growth velocity. There is some indication that it is species-characteristic and varies with other measurable characters. The variables a and t_0 are not the same for L and $W^{\frac{1}{3}}$, and the conversion from one set of units to the other is poorly defined. Work by Frazer and Hugget (1973) indicates that, at least for a, the relationship is *not* simply linear (i.e. not convertible by a common 'factor').

Estimation of (t_g–t_0) requires a dependable estimate of length at birth. This in turn requires a series of specimens in sizes bracketing the true birth size. Length at birth can be estimated by interpolation as shown for *Stenella attenuata* by Perrin, Coe and Zweifel (1976) (also see below). In some cases a mean is calculated, in others the median is used. Both should be adequate if the real distribution of points is symmetrical. This method also requires an accurate separation of modes in size in a large data series. When modes are not distinct, this is undoubtedly a poor method. In some cases individuals are plotted rather than modes. This should be valid if breeding is distinctly seasonal.

Estimation of the early phase t_0 is not straightforward or well defined. All applications refer back to Hugget and Widdas' (1951) simple breakdown of the proportion of gestation time in t_0 by length of (t_g–t_0). For example, for (t_g–t_0) > 400 days, they said that t_0 should be approximately $0.1 \times t_g$. Laws (1959) defined the relationship for length as being about 90% of that for weight. Both rules of thumb are arbitrary. Hugget and Widdas proposed the original scheme based on data from only seven species of terrestrial mammals. They extrapolated outside the limits of their data for the extreme values ($t_g > 400$). Gestation periods for many delphinids lie outside the data range used by Hugget and Widdas.

A more precise definition of t_0 is needed. As

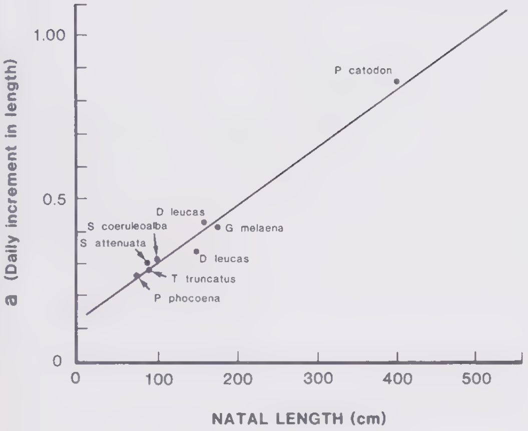

Fig. 2. Interspecific relationship between fetal growth rate (a) and natal length, from Kasuya (1977).

mentioned above there appears to be a reasonably consistent relationship between *a*, (the slope of the linear phase) and size at birth. As shown in Fig. 2 (from Kasuya, 1977), the relationship appears to be linear, although the sample size employed is not large.

This relationship has been employed to estimate *a* for *Pseudorca crassidens* (Purves and Pilleri, 1978) and the non-delphinids *Pontoporia blainvillei* (Kasuya and Brownell, 1979) and *Berardius bairdii* (Kasuya, 1977). With this comparative slope estimate and an estimate of length at birth, the Hugget and Widdas procedure can be carried out. Unfortunately the large data series required for direct estimation of *a* is also generally required for a good estimate of natal length, so this relationship is of limited use.

Method of Sacher and Staffeldt (1974). The second type of statistical estimation is based on an empirically defined relationship between the duration of gestation and brain weight at birth, the ratio of birth to adult brain weight, and litter size. Sacher and Staffeldt examined a data series on 91 species of eutherian mammals. Variables included in the multiple-regression analysis were the above, plus (1) body weight at birth and (2) ratio of birth weight to adult body weight. The body-weight variables were not significantly related to gestation period. In applying this method one simply uses natal brain weight and litter size in the multiple-regression model. Our reservations about this procedure include the following:

(1) Only two cetacean species were included in the 91 species from which the model was derived (*Tursiops truncatus* and *Phocoena phocoena*).
(2) The use of data across many orders is useful in defining general patterns but probably does not provide good prediction within a particular order.
(3) Use of ratios which include another predictor variable in the model is of questionable validity as a statistical technique.
(4) Variables included in the original study were limited in scope; but R^2 was high (> 0.9).

Comparative G vs L_n. The third statistical approach utilizes the apparent relationship between duration of gestation (G) and size at birth (L_n) for other species within the Delphinidae (Fig. 3). Perrin, Miller and Sloan (1977) utilized this for *S. longirostris*. There was a fairly good fit by a straight line, but as with the other comparative relationship, the sample size available was not large.

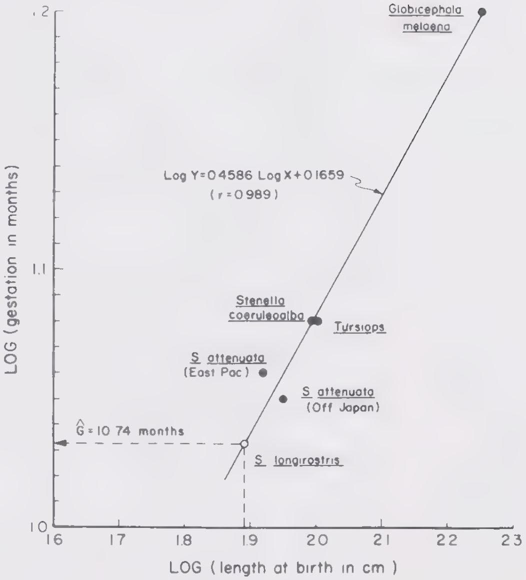

Fig. 3. Interspecific relationship between duration of gestation and size at birth, in four delphinid cetaceans, with extrapolation to predict length of gestation in the eastern spinner dolphin (from Perrin *et al.* 1977).

C. Other methods

These are generally visual fits to apparent modes in length frequencies or in frequencies of parturition or conception, e.g. *L. acutus* (Sergeant, St Aubin and Geraci, 1980) and *D. delphis* (Kleinenberg, 1956). This type of method may be a good first approximation for small data series but should be replaced by more quantitative, repeatable methods where possible.

Lastly, for nine species, estimates of gestation period were published with no accompanying information on data methods or sources.

Available estimates

The published estimates of gestation period range from about 10 months to over 16 months (Table 2). As discussed above, there appears to be a relationship between length of gestation, fetal growth rate and birth size or brain weight at birth, such that larger delphinids (e.g. *Orcinus* and *Globicephala*) have longer gestation periods than do the smaller forms (*Stenella* or *Lagenorhynchus*).

There is an apparent contradiction between the results of Sacher and Staffeldt (1974) and those of the other statistical studies discussed here. They found no significant relationship between body size and gestation period. It would be of interest to pursue this disparity further, since the majority of comparative estimates (not just for delphinids) appear to utilize the body size/gestation relationship in some way.

Table 2

Gestation periods reported for delphinid cetaceans. Method types are defined in Table 1

Species	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source	Estimate (months)	Method type	Source
Sotalia fluviatilis	10.0–10.3	III	Best and da Silva, 1984						
Tursiops truncatus	12	I	Essapian, 1963	12	I	McBride and Kritzler, 1951	12	I	Tavolga and Essapian, 1957
	13	IV	Perrin *et al.*, 1977						
('*aduncus*')	11.5–12	I	Ross, 1977						
Globicephala melaena	15.2	III	Sergeant, 1962	16.2	V	Sergeant, 1962	15.7	III	Frazer and Hugget, 1973
	15–16	VII	Harrison, 1969						
G. macrorhynchus	12	VII	Lowry, 1974						
Stenella attenuata	11.5	III	Perrin *et al.*, 1976	11.2	III	Kasuya *et al.*, 1974	9–10	VII	Harrison, 1969
S. longirostris	10.7	Va	Perrin *et al.*, 1977	9.5, 10.5	IV	Perrin *et al.*, 1977			
S. coeruleoalba	12	VI	Kasuya, 1972						
Delphinus delphis	10–11	VI	Kleinenberg, 1956	10	VII	Tomilin, 1957	11	VII	Harrison, 1969
	10	VII	Mal'm, 1932						
Pseudorca crassidens	15.5	III	Purves and Pilleri, 1978	11–12	VII	Harrison, 1969			
Orcinus orca	12–16	VI	Nishiwaki and Handa, 1953	12	II	Guldberg and Nansen, 1894	12	VII	Fraser, 1937
	12	VII	Grieg, 1889	11–12	VII	Harrison, 1969	12	VII	Christensen, 1984
'best'	15	I, VII	Perrin (ed.), 1982						
Lagenorhynchus acutus	10	II	Guldberg and Nansen, 1894	10	VII	Fraser, 1937	11	VI	Sergeant *et al.*, 1980
	11–12	VII	Geraci and St. Aubin, 1977						
L. obliquidens	10	VII	Harrison, 1969						
			(Comparative estimates for other odontocetes)						
Phocoena phocoena	11	III	Laws, 1959	9	VII	Harrison, 1969			
Pontoporia blainvillei	11	III	Kasuya and Brownell, 1979	10.5–12	Va	Kasuya and Brownell, 1979			
Berardius bairdii	17	V	Kasuya, 1977	10	VII	Harrison, 1969			
Delphinapterus leucas	12	VII	Vladykov, 1944	14	III	Laws, 1959			
Physeter macrocephalus	16	III	Laws, 1959	16–17	VII	Harrison, 1969			

Size at Birth

Estimates of size at birth are used in estimating the length of gestation and the time of birth. They are also the starting point for growth curves and ultimately contribute to estimates of the reproductive capacity of a population.

There are two basic categories of methods used to estimate length at birth. One quantitative method which has been employed for delphinids is termed '50% interpolation' in Table 3. In this method, the percentage of specimens which are postnatal is plotted for length categories or for length modes. The point on the length axis which corresponds to 50% postnatal from a linear regression is defined as the estimate of length at birth. The basic assumptions of the method are that (1) pregnant females (i.e. fetuses) and calves are equally available to the sampling procedure used, (2) both suffer natural mortality at the same rate, (3) naturally born calves are accurately distinguished from aborted, near-term fetuses, and (4) the sample size is adequate.

A second quantitative method used to determine size at birth is calculation of the mean length in a sample of apparently newborn calves. This method assumes that newborn calves are easily distinguishable from slightly older individuals. It will usually overestimate size at birth, especially if the calving season is protracted.

The other category of methods can be roughly termed 'qualitative' in that they don't use statistical techniques. One common method is to examine a relatively small series of fetuses and newborn calves, note the lengths and qualitatively infer a likely intermediate value for length at birth. Another is to use the length of the smallest postnatal specimen. (See Appendix 1 for smallest calf and largest fetal lengths reported.) For a number of other populations the methods used to arrive at the reported birth length were not reported. There is a total of 28 estimates available for 14 of 32 delphinid species (Table 3).

Of the methods discussed, the 50%-interpolation method is preferable. The assumptions of the method should be closely examined for each situation, however. Hohn and Hammond (1983) have discussed the basic methods for estimating length at birth in detail.

Size and Age at Attainment of Sexual Maturity

Age at attainment of sexual maturity is an important parameter in stock assessment because it is thought to vary with exploitation, as part of the density-dependent response that theoretically yields a net reproductive rate greater than zero (Smith, 1983). Such change has not been observed but it has been inferred to have occurred in some

Table 3

Body lengths at birth reported for delphinids

Species and region	Length at birth (cm)	Method	Source
Sotalia fluviatilis	75	Qualitative interpolation	Best and da Silva, 1984
Stenella coeruleoalba			
(Japan)	99.8	50% interpolation	Kasuya, 1972
(Japan)	100	50% interpolation	Miyazaki, 1977
S. attenuata			
(Japan)	89	Mean length of 'newborns' in drive fishery	Kasuya *et al.*, 1974
(E. trop. Pacific)	82.5	50% interpolation	Perrin *et al.*, 1977
S. longirostris			
(E. trop. Pacific)	77	50% interpolation	Perrin *et al.*, 1977
Delphinus delphis			
(E. trop. Pacific)	81.3	50% interpolation	Hui, 1977
(E.N. Pacific)	79.0	50% interpolation	Hui, 1977
(Black Sea)	80–90	Not reported	Tomilin, 1957
(All)	105	Not reported	Scott, 1949
Globicephala melaena			
(W.N. Atlantic)	177	50% interpolation	Sergeant, 1962
G. macrorhynchus			
(W. Pacific)	135–146	Range in size of 'newborns'	Yonekura *et al.*, 1980
(S. Africa)	140	Qualitative inference from small sample	Ross, 1979
Lagenorhynchus acutus			
(W. Atlantic)	110	Method not reported	Sergeant *et al.*, 1980
L. albirostris			
(E.N. Atlantic)	125	Method not reported	Tomilin, 1957
Orcinus orca			
(Japan)	276	Smallest postnatal specimen	Nishiwaki and Handa, 1958
(N. Atlantic)	210	Qualitative inference from fetal and calf lengths	Jonsgård and Lyshoel, 1970
(NE. Pacific)	246	Direct observations of five stranded newborn	Bigg, 1982
(N. Atlantic)	208–220	Qualitative extrapolation from fetal development	Guldberg and Nansen, 1894
(All?)	210–250	Not reported	Tomilin, 1957
Pseudorca crassidens			
(All?)	193	Mean length youngest calves	Purves and Pilleri, 1978
(S. Africa)	160	Qualitative inference from few specimens	Ross, 1979
Tursiops truncatus			
(W.N. Atlantic)	100	Not reported	Sergeant *et al.*, 1973
(W.N. Atlantic)	115	Average length of 'true neonates'	Hohn, 1980
(All)	980–1260	Range of reports	Harrison, 1969
(?)	130	Not reported	Scott, 1949
(S. Africa '*aduncus*')	838–1120	Range of eight specimens	Ross, 1977
Sousa chinensis			
(S. Africa)	100	Qualitative inference from specimen series	Ross, 1979
Grampus griseus			
(All?)	150	Not reported	Tomilin, 1957
(Japan)	110–120	Qualitative inference from specimen series	Mizue and Yoshida, 1962

instances, based on comparison of populations of one species (*Stenella longirostris* – Perrin and Henderson, 1984) or populations of two species (*S. coeruleoalba* and *S. attenuata* – Kasuya, 1976) with different histories of exploitation.

Knowledge of size at maturation is useful because it allows estimation of maturity status of animals for which only length data are available.

Definition and criteria of sexual maturity

For females, the most accepted definition of sexual maturity is that the animal has ovulated at least once, as evidenced by presence of at least one corpus luteum or corpus albicans in the ovaries. The assumption is made that scars of ovulation (whether or not followed by pregnancy) remain visible in the ovaries indefinitely (see Perrin and Donovan, 1984). An additional assumption commonly made is that presence of any scar or body in the ovaries means that ovulation has occurred (e.g. Perrin *et al.* 1976). This is not a valid assumption, because some scars may denote non-ovulatory events, e.g. lutealization of unerupted Graafian follicles (Perrin and Donovan, 1984).

For males the question of what constitutes sexual maturity is more complex. Several criteria have been used in population studies. Presence of spermatozoa in the center of the testis was employed by Kasuya, Miyazaki and Dawbin (1974). Miyazaki (1977) defined immature, pubertal and mature males as those having, respectively, no spermatozoa, both spermatogonia and spermatocytes, and spermatozoa in the center of the testis. Perrin *et al.* (1976) defined puberty and maturity based on presence of spermatogenesis in the center of the testis, rapid change in diameter of seminiferous tubules, and presence of spermatozoa in the epididymis. Perrin *et al.* (1977) and Perrin and Henderson (1984) defined several levels of sexual 'maturity' based on presence of spermatogenesis and amount of sperm in the epididymis. Sergeant (1962) defined the onset of 'functional' maturity as the point at which gross examination of the epididymis shows presence of seminal fluid, which occurs at testis weights somewhat greater than those at which spermatogenesis can be detected histologically. Other workers have used various combinations of these criteria; this, as well as the use of various estimation procedures - described below – must be kept in mind when making comparisons of estimates of size or age at attainment of maturity across species or across studies.

An assumption made in the use of presence of sperm in the epididymis as a criterion of sexual maturity is that adult males produce sperm on a constant basis. This assumption is not valid, as it has been shown in at least some species that males may enter a resting phase, during which testis size decreases and sperm are absent from the epididymis (Hirose and Nishiwaki, 1971; Perrin and Henderson, 1984; Collet and St Girons, 1984).

Estimation methods

Length and age at attainment of maturity in females have been estimated in various ways:

- (*a*) *The mean length or age when 50% are mature*, by inspection of data tabulated by length or age interval (Mayarova and Danilevskiy, 1934; Sergeant, 1962) or by estimation of the 50%-mature length (or age) from a line fitted to a plot of % mature on length or age intervals (Kasuya, 1972; Perrin *et al.*, 1976; Perrin *et al.*, 1977). Perrin *et al.* (1976) noted that an estimate obtained in this way is an overestimate, because some of the smaller mature animals are those that have stopped growing at a shorter-than-average length, yielding an asymmetrical (left-skewed) maturity-length curve.
- (*b*) *The length or age at which the number of smaller or younger mature females equals the number of larger or older immature females.* Kasuya *et al.* (1974) pointed out that an estimate by this method is biased downward, because it does not take into account the effect of natural mortality in reducing the relative number of longer or older animals.
- (*c*) *The length or age corresponding to the age or length at which 50% are mature*, taken from an age-length key or growth curve (Kasuya *et al.*, 1974; Perrin *et al.*, 1976).
- (*d*) *The average greatest length at which females have not yet ovulated*, estimated by back-extrapolation to the origin of a body-length/corpus-count curve (Perrin *et al.*, 1976). Average age at maturity can then be estimated from a length/age curve.
- (*e*) *The length at first conception*, estimated in gravid females with only one ovarian corpus (a corpus luteum). A length increment (taken from a length/age curve) corresponding to the estimated time since conception as estimated from the length of the fetus (taken from a fetal length/age curve) is subtracted from body length (Perrin *et al.*, 1976). Average age at maturity can then be taken from a length/age curve. This is a probable underestimate, because it is based only on females that become pregnant at the first ovulation.

DeMaster (1984) has examined the properties of these estimates in more detail.

Average length and testis weight at age at attainment of sexual maturity in males have been estimated by some of the same methods used for females (*a*, *b* and *c* above). In more recent studies, e.g. Perrin *et al.* (1977) and Perrin and Henderson (1984), values have been estimated for several indices of 'maturity' (described above), with the caution that not enough is known about the breeding systems of these animals at any particular length, age, testis size, etc., to say that they are 'socially mature' in the sense of Best (1969a).

Available estimates

Estimates of age at attainment of sexual maturity are available for 11 of the roughly 32 species of delphinids (Table 4). They range from 3 (*Delphinus delphis*) to 16 years (*Orcinus orca*). (The former is almost certainly an underestimate, due to the effects of schooling segregation – see discussion below.) In many cases only a fairly broad range of estimates is available (e.g. 8–14 years for *Pseudorca crassidens*), which highlights the rudimentary state of knowledge of the life histories of most of the delphinids. Additional data on testis weight (of smallest 'adult' testis and of largest testis) and on body length (largest sexually immature and smallest mature animals) are included in Appendices 2 and 1, respectively. It should be noted that many species vary in these parameters from region to region (discussed below).

Average Size and Age of Adults

Average adult size and age are other parameters that may change under exploitation, with changes in age structure of the population caused by selective harvest or by increased reproductive rates. Average size and age are also useful parameters in cross-species comparisons and deductive modeling (discussion below). Available estimates of average adult length and age are given in Appendices 3 and 4, respectively.

Maximum Size and Age and Asymptotic Length

These parameters are useful in deductive modeling of life history. Asymptotic length is important in any model of growth. Values of maximum size based on adequate samples ($n \geqslant 25$) are available in the literature for about half the delphinid species (Appendix 1). The wide geographical variation apparent in some species is discussed below. Maximum ages based on large samples are available for only a handful of species (Appendix 4) and in many cases are expressed in terms of dentinal or cemental growth-layer groups (GLGs, terminology of

Table 4

Estimates of average length and age at attainment of sexual maturity and ages of oldest immature and youngest immature for delphinids. Sample sizes in parentheses; values rounded off to nearest year (y) or GLG – terminology of Perrin and Myrick 1980 – (G)

Species and region (stock in parentheses)	Average length at attainment of sexual maturity		Average age at attainment of sexual maturity		Oldest immature animal		Youngest mature animal		Source
	Male	Female	Male	Female	Male	Female	Male	Female	
Steno bredanensis									
W. North Pacific	—	—	—	—	—	—	14G (9)	17G (9)	Miyazaki, 1980
Peponocephala electra									
W. South Pacific	—	—	—	—	3G (1)	4G (2)	7G (3)	12G (1)	Bryden *et al.*, 1977
Pseudorca crassidens									
E. North Atlantic	396–457	366–427	8–14y	8–14y	—	—	—	—	Purves and Pilleri, 1978
W. North Pacific	—	380–399	—	—	—	—	—	—	Kasuya and Izumisawa, 1981
Orcinus orca									
E. North Atlantic	~ 579	457–488	~ 16y	~ 10y	—	—	—	—	Christensen, 1982; Jonsgård and Lyshoel, 1970
Globicephala melaena									
W. North Atlantic	490	365	12y	6–7y	15y (13)	6y (5)	11y (19)	5y (12)	Sergeant, 1962
G. macrorhynchus	—	380–390	—	—	—	14G (2)	12G (2)	11G (1)	Ross, 1979
Lagenorhynchus obliquidens									
E. North Pacific	170–180	—	—	—	—	—	—	—	Harrison *et al.*, 1972
L. obscurus									
E. South Atlantic	—	—	—	—	—	—	—	18y	Best, 1976
L. actus									
W. North Atlantic	230–240	201–222	—	—	—	12y (6)	—	6y (26)	Sergeant *et al.*, 1980
Tursiops truncatus									
Both coasts of Florida	245–260	220–235	~ 11y[1]	~ 12y[1]	20y (10)	14y (11)	12y (6)	9y (17)	Harrison *et al.*, 1972; Leatherwood *et al.*, 1978; Sergeant *et al.*, 1973
S.W. Indian Ocean ('*aduncus*')	210–240	213–230	9–11G	—	4G (7)	4G (6)	9G (11)	10G (6)	Ross, 1979
Grampus griseus									
S.W. Indian Ocean	—	—	—	—	3G (4)	5G (4)	—	> 9G (1)	Ross, 1979
Stenella longirostris									
Gulf of Mexico	~ 190	~ 188	—	7–10G	> 8G (3)	> 11G (7)	> 9g (8)	> 8G (4)	Mead *et al.*, 1980
E. trop. Pac. (eastern)	160–170	164	6–9y	4–5y	8 9y (106)	6 9y (94)	5 7y (106)	3 5y (153)	Perrin *et al.*, 1977
E. trop. Pac. (n. whitebelly)	165–170	167	6–8y	4–6y	11–16y (48)	7–11y (37)	4–5y (52)	3–4y (150)	Perrin and Henderson, 1984
S coeruleoalba									
E. trop. Pacific	195–200	—	—	—	—	—	—	—	Gurevich and Stewart, 1979
W. North Pacific	219	216	9y	9y	12y (70)	13y (126)	7y (222)	5y (541)	Miyazaki, 1977
S.W. Indian Ocean	210–220	—	—	—	13+G (5)	3G (1)	12+G (2)	7G (2)	Ross, 1979
S. attenuata									
E. trop. Pac. (offshore)	~ 195	181	11G	8G	13G (55)	11G (100)	7G (42)	7G (209)	Perrin *et al.*, 1976
W. North Pacific	194	182	12y	9y	16y (81)	12y (69)	8y (49)	8y (124)	Kasuya, 1976; Kasuya *et al.*, 1974
Delphinus delphis									
Black Sea	170–180	150–170	3y	(a) 4y (b) 2y	—	—	—	—	Kleinenberg, 1956; Kleinenberg and Klevezal', 1962; Mayarova and Danilevskiy, 1934; Sleptsov, 1941
E. North Atlantic	200	190	5–7G	6–7G	—	—	—	—	Collet, 1981
E. trop. Pac. (cent. trop.)	200	—	6–7G	—	—	—	—	—	Gurevich and Stewart, 1978; Oliver, 1973
E. North Pacific	—	—	7–12y	—	12y (21)	14y (9)	9y (10)	8y (19)	Hui, 1977
S.W. Indian Ocean	—	—	—	—	12G (3)	8G (6)	11+G (2)	10G (1)	Ross, 1979

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[1] From N.E. Florida.

Perrin and Myrick, 1980) that have not yet been calibrated to real time. The greatest ages reported in terms of years are for *Stenella attenuata* (40 years for males and 46 years for females) and in GLGs for *Peponocephala electra* (47 GLGs for males).

Adequate estimates of asymptotic length are available for even fewer species (Appendix 3). In most cases it has been estimated simply as the average length of physically mature specimens (those in which the vertebral epiphyses are fused to the centra and which are presumed to have stopped growing in length). In cases where the authors presented length data for physical maturity but did not estimate asymptotic length, we carried out the calculation and included the value in Appendix 3.

Perrin *et al.* (1976) estimated asymptotic length in *Stenella attenuata* as the average length of specimens in which the pulp cavity of the tooth was occluded. They used this estimate in fitting a Gompertz model of growth to their data. In similar development of a growth model, Perrin *et al.* (1977) estimated asymptotic length for *S. longirostris* (eastern form) as the average length of animals with 13 or more dentinal GLGs. Kasuya (1976) estimated asymptotic length in *S. attenuata* and *S. coeruleoalba* (later revised upward by Miyazaki, 1977) as the length at which growth rate levels off, based on growth curves fitted to length/age data by eye. Perrin and Henderson (1984) estimated asymptotic length for the northern whitebelly form of *S. longirostris* with iterative fits of Gompertz models to age/length data. This last method involves the fewest assumptions and is probably the most appropriate of those discussed here, providing that the sample includes adequate numbers of older animals.

Ovulation Rate

Background and estimation methods

The ovaries of cetaceans are unusual in that scars (corpora albicantia, or CAs) resulting from ovarian events persist for years and probably indefinitely in at least some species. Early on, it was thought by some workers (e.g. Sleptsov, 1941) that CAs persist indefinitely in all delphinids, that they result only from regression of corpora lutea (CLs) of pregnancy, and that there is never more than one CL per pregnancy. This supposedly resulted in a permanent record of the number of pregnancies experienced by a particular female. The potential value of such a record, coupled with accurate age determination, in modeling population dynamics for stock assessment and management is obvious, but more recent research has shown that the genesis and significance of ovarian scars are more complex than earlier thought (see sections II A and B and Appendix B of Perrin and Donovan, 1984). CAs do apparently persist indefinitely in at least some species, e.g. *Globicephala macrorhynchus* (Marsh and Kasuya, 1984) and perhaps *G. melaena* (Sergeant, 1962). In *Tursiops truncatus*, CAs resulting from several successive infertile ovulations in females just entering sexual maturity may be resorbed (Harrison *et al.*, 1972). In *Stenella* spp. (*S. attenuata*, *S. longirostris* and *S. coeruleoalba*) the data are equivocal. Some apparently senescent females have withered ovaries containing fewer CAs than do the ovaries of some other younger females still reproductively active, indicating that some CAs may eventually be resorbed, or at least not detected with the methods used to examine the ovaries in most studies (Perrin *et al.*, 1976; 1977; Kasuya, 1976; Perrin and Donovan, 1984). CAs of infertile ovulation may be more likely to be resorbed than those of pregnancy (Harrison *et al.*, 1972). In any case, for most delphinids there is no assurance that the CAs represent a complete history of ovarian activity.

All CAs do not represent pregnancies; some are the result of regression of CLs of infertile ovulation (Harrison *et al.*, 1972; Benirschke, Johnson and Benirschke, 1980). Although CAs of pregnancy may be more likely to persist indefinitely than those of simple ovulation, there is the problem of distinguishing between the two types of CAs. Some workers (e.g. Ivashin, 1984) maintain that this can be done based on histological criteria, but the balance of scientific opinion holds that CAs of pregnancy cannot be distinguished from those of infertile ovulation with present knowledge (Perrin and Donovan, 1984).

There may be more than one CL per pregnancy. Multiple CLs are common in some odontocetes (e.g. monodontids, Brodie, 1972) but rare in delphinids (loc. cit.).

Although ovarian scars do not provide a reliable record of fecundity, they are, at least for younger animals, a relative index of ovarian activity, i.e. estrus and ovulation, and thus potentially are still valuable in characterizing the structures, breeding systems and dynamics of populations. The somewhat controversial question of spontaneous vs induced ovulation is relevant to interpretation of CAs and estimation of ovulation rate. Harrison (1969) and Harrison *et al.* (1972) concluded that some delphinids (e.g. *Globicephala melaena*, *Pseudorca crassidens*, and perhaps *Stenella* spp. and *Lagenorhynchus obliquidens*) are probably spontaneous ovulators, but that others, in particular *Tursiops truncatus*, are reflex ovulators, i.e. require copulation and/or presence of a mature male to trigger ovulation. This and similar conclusions by Saayman and Taylor (1977) and Ross (1977) are based mainly on data for captive animals, i.e. observations that the ovaries of some captive females that have not been kept with adult males contain very few or no CAs despite having been of adult size and age for several years. In view of more recent work, however, it seems likely that these low rates or absence of ovarian activity may be related to other aspects of captivity. Longitudinal monitoring and experimentation have now shown clearly that both *Delphinus delphis* and *Tursiops truncatus* in captivity are spontaneous, albeit sporadic, ovulators (Kirby and Ridgway, 1984), and results of analyses of ovaries of *Stenella attenuata* and *S. longirostris* suggest that these dolphins ovulate spontaneously in the wild (Benirschke *et al.*, 1980), perhaps with more regularity than observed for other species in captivity. This endogenicity and regularity makes corpus-count data from wild populations potentially more valuable in modeling than would otherwise be the case.

Another important consideration in estimating ovulation rate from corpus-count data is that of variation with age. Models of ovulation rate that employ a linear fit to corpus-count/age data (e.g. Kasuya, 1972, for *Stenella coeruleoalba*; Kasuya, 1976, for *S. coeruleoalba* and *S. attenuata*) assume no change in ovulation rate with age, but these linear fits are not good; inspection of the data shows systematic underestimation of rates in very young females and overestimation for old females. Curvelinear models (Perrin *et al*., 1976; Perrin *et al*., 1977; Perrin and Henderson, 1984) fit the data better and are consonant with data for captive animals, which indicate that young females may ovulate two or more times in relatively quick succession when entering sexual maturity (Harrison *et al*., 1972). Data for old females indicate that some are reproductively senescent (Perrin *et al*., 1976; Marsh and Kasuya, 1984). A typical pattern is that in *S. attenuata* (Perrin *et al*., 1976) of 4 ovulations in the first year of sexual maturity, 2 in the second, and about 1 per year thereafter, until some time beyond about 13 years of reproductive age, when some individuals become senescent. In some other populations (e.g. *Stenella longirostris* – Perrin *et al*., 1976) the rates for very young females are only slightly higher than for older females. As pointed out by Perrin *et al*. (1976) and Kasuya *et al*. (1974), estimates for ages beyond about 12 years have been unreliable because of underestimation of age caused by difficulty in interpreting very thin and convoluted dentinal GLGs in older animals.

Another source of error in corpus count/age data is the inclusion of corpora atretica and other scars of non-ovulatory events in the corpus-count (e.g. Perrin *et al*., 1976 and 1977; Perrin and Henderson, 1984). The count should include only CLs and CAs (Perrin and Donovan, 1984).

In fitting models to corpus-count/age data to estimate ovulation rates, individual variation in age at attainment of sexual maturity must be taken into consideration. If the relationship of % mature to age is a symmetrical S-shaped curve and the curvilinear fit to corpus-count/age data is unweighted, this factor does not affect the analysis. In some instances, however, e.g. in the 'eastern' population of *Stenella longirostris* in the eastern Pacific (Perrin and Henderson, 1984), the maturation curve is quite skewed, and in such cases allowance for individual variation in age at maturation should be incorporated in the model. Perrin *et al*. (1976 and 1977) and Perrin and Henderson (1984) estimated average reproductive age $\bar{A}$ for an age interval p as

$$\bar{A} = \left(\sum_{i=1}^{p} a_i b_i\right) \div c$$

where $a_i = \%$ maturing in ith interval (% mature in i minus % mature in $i-1$); $b_i =$ average reproductive age in interval p of females mature in i; and $c = \%$ mature in interval p. Average reproductive age in the ith interval of females maturing in i was set at 0.50.

Another method of estimating ovulation rate is based on estimated ages of CAs as indicated by size and other indices of degree of regression of the CL (Sergeant, 1962; Kasuya, 1972; Kasuya *et al*., 1974). As pointed out by Kasuya (1976) and Miyazaki (1977), this method is not satisfactory for the delphinids because size of a CA is not a reliable index of its age, beyond the very early stages of regression of the CL.

Any use of estimates of ovulation rate in modeling (e.g. application to a corpus-count frequency distribution to obtain an age-frequency distribution) should only be done keeping in mind the very great individual variation in ovulation rate and resulting relatively low precision of the estimator. As can be seen in any scatterplot of corpus-count on age for a wild population (Kasuya, 1972; Kasuya *et al*., 1974; Perrin *et al*., 1976 and 1977; Sergeant *et al*., 1980), variation can be sixfold or greater even among fully-mature females. Rates for adult captive animals of the same species kept under the same conditions can range from none to several ovulations per year (Wells, 1984; Kirby and Ridgway, 1984). Thus, corpus count is not a reliable predictor of age for individual animals, and any population index based on it will have an extremely large variance.

Available estimates

The available estimates of ovulation rates (Table 5) vary broadly among the delphinids. They also vary considerably within a species, depending on region and on the model employed. The curvilinear models are more consonant with the estimates based on direct observations than are the linear models. The difference between the estimates for the two stocks of *Stenella longirostris* is discussed below in the section on effects of exploitation.

Pregnancy Rate and Calving Interval

Estimation methods

Annual pregnancy rate (APR) is usually estimated as the percentage of mature females pregnant (including those that are simultaneously pregnant and lactating) divided by the length of gestation (expressed in years). Several assumptions are implicit in this simple model:

(a) There is no sampling bias caused by selectivity, i.e. the distribution of reproductive conditions in the sample is the same as in the population sampled. Factors that can invalidate this assumption include differential vulnerability (e.g. pregnant females easier to catch) and school or areal segregation by age or reproductive condition (e.g. more 'breeding' schools sampled than other types of schools). The latter factor is discussed below.

(b) There is no sampling bias caused by seasonality of calving (also discussed below).

(c) All pregnancies are detected. A very small embryo can be overlooked, especially in the field. If presence of a corpus luteum (CL) is used as a criterion of pregnancy, the estimate of APR is biased upward, because not all CLs derive from pregnancies and some pregnancies result in more than one CL (Perrin and Donovan, 1984).

APR can also be estimated as the reciprocal of calving interval (CI) calculated as the sum of independent estimates of the lengths of the component phases of the reproductive cycle: gestation, lactation (discussed below) and 'resting' (time spent neither pregnant nor lactating). The estimate of the length of the cycle obtained this way must be adjusted downward to take into account any overlap of lactation and pregnancy, by a factor equal to

Table 5

Ovulation rates in delphinids

Species and region (stock in parentheses)	Rate (ovulations/year or GLG)	Model/method	Source
Pseudorca crassidens			
E. North Atlantic	Possibly several/y	—	Comrie and Adams, 1938
E. North Atlantic	About one/y	—	Purves and Pilleri, 1978
Globicephala melaena			
W. North Atlantic	2.4–2.5/y	—	Sergeant, 1962
Lagenorhynchus obliquidens			
E. North Pacific	High compared to other delphinids	—	Harrison *et al.*, 1972
L. acutus			
W. North Atlantic	> 1/y	—	Sergeant *et al.*, 1980
Tursiops truncatus			
W. North Atlantic	~ 1/GLG after ~ 15 GLGs	—	Sergeant *et al.*, 1973
Not given (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984
Stenella longirostris			
E. trop. Pacific (eastern)	~ 1/GLG, declining slightly with age	$Y = 1.39X^{0.79}$	Perrin *et al.*, 1977
E. trop. Pacific (eastern)	Same	$Y = 13.68\,(i - e^{-0.099x})$	Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	~ 3/first GLG, 2/second, falling off rapidly to < 1/GLG.	$Y = 6.80\,(i - e^{-0.654x})$	Perrin and Henderson, 1984
Central Pacific (captive)	Several/y	Direct observations	Wells, 1984
S. coeruleoalba			
W. North Pacific	0.69/y (0.25 to 1.6)	$Y = 0.69X - 5.16$	Kasuya, 1972
W. North Pacific	0.59/y, between 10 and 15y	$Y = 0.590X - 4.875$	Kasuya and Miyazaki, 1975
W. North Pacific	0.41/y, between 5 and 25y	$Y = 0.414X - 2.40$	Kasuya, 1976
	0.12/y, between 26–43y	$Y = 0.115X - 6.55$	Kasuya, 1976
W. North Pacific	~ 3/y (1.5 to 12)	Ovary diagram	Miyazaki, 1977
S. attenuata			
W. North Pacific	0.43, increasing slightly with age	$Y_t = 0.00327X_t + 0.4286$	Kasuya *et al.*, 1974
W. North Pacific	0.41/y	$Y = 0.412X - 1.97$	Kasuya *et al.*, 1974
E. trop. Pacific (offshore)	~ 4/first GLG, 2/second, falling off to ~ 1/GLG	$Y = 4.06X^{0.51}$	Perrin *et al.*, 1976
Delphinus delphis			
E. North Pacific (captive)	None to several/y	Direct observations	Kirby and Ridgway, 1984

the percentage of lactating females also pregnant (Perrin *et al.*, 1977).

An approximate variance of the APR has been estimated (e.g. Perrin *et al.*, 1977) as

$$\mathrm{var}\,(\mathrm{APR}) = \mathrm{APR}\,(1 - \mathrm{APR})/n$$

which is the variance of a simple proportion. Since the basic APR estimate includes adjustment of the proportion pregnant (P) by the gestation period in years (T_G), the above method will generally underestimate var (APR). A better approximation of var (APR), using the delta method (Seber, 1973), is

$$\mathrm{var}\,(\mathrm{APR}) = (-P/T_G^2)^2\,\mathrm{var}\,(T_G) + (1/T_G^2)\,P(1-P)/n_p,$$

where n_p is the sample size used to estimate P. This assumes that P and T_G are independently estimated, i.e. $\mathrm{cov}\,(P, T_G) = 0$ and, on a more practical level, that an estimate of the variance of T_G exists. While gestation period is one of the least variable vital parameters, estimation of T_G is usually not straightforward and variances have not been estimated in most cases (see 'Gestation period and fetal growth rate,' above).

The above does not hold for APR estimated as the reciprocal of the sum of the component phases of the reproduction cycle. This estimate of APR and its variance are more complex and dependent upon unbiased estimates of not only the proportion pregnant, but those lactating and in gestation. Also, pregnancy rate estimated by this second method is systematically negatively biased (L. L. Eberhardt, personal communication to WFP, 2/13/80).

The variance of the calving interval estimate can also be derived using the delta method. With CI = 1/APR, the approximate variance is

$$\mathrm{var}\,(\mathrm{CI}) = (\mathrm{APR}^{-4})\,\mathrm{var}\,(\mathrm{APR}).$$

Available estimates

Estimates of APR are available for only a few species (Table 6). They range from 12% (from the data of Jonsgård and Lyshoel, 1970, for *Orcinus orca* in the North Atlantic) to about 75% (*Tursiops truncatus* and *Delphinus delphis* in the Black Sea). In some cases where two or more estimates are available for the same population, they vary by a factor of about two or more (*Orcinus orca*, *Stenella coeruleoalba* and *Delphinus delphis*). At least some of this variation must be due to violation of the above-listed assumptions. In the case of the Black Sea (*Tursiops truncatus* and *Delphinus delphis*), Kleinenberg (1956) pointed out that calving females apparently leave the area of the fishery and remain apart during early lactation, thus causing a downward bias in the estimated length of lactation and an upward bias in APR. The estimate of APR for the Black Sea population

Table 6

Estimates of annual pregnancy rate (APR) and calving interval (CI) for delphinids. Criterion of pregnancy noted as fetus present (F) or corpus luteum present (CL). Method for estimating APR noted as percentage of mature female pregnant P divided by gestation period G expressed in years (P/G); as reciprocal of sum of separately estimated reproductive phases (S); or as inferred from several lines of evidence (I). Estimates of calving interval CI noted as reciprocal of APR or of sum of phases S

Species and Region (stock or years in parentheses)	Mature females (no.)	Percent pregnant P (and criterion) (%)		Annual pregnancy rate APR (and method) (%)		Calving interval CI (and method) (years)		Source of estimates or data
Pseudorca crassidens								
E. North Atlantic	(59)	14.0	(F)	—	—	—	—	Purves and Pilleri, 1978
W. North Pacific	(38)	21.1	(F)	—	—	—	—	Kasuya and Izumisawa, 1981
Orcinus orca								
E. North Atlantic	(430)	13.7	(F)	12.0	(P/G of 15 months)	8.3	(1/APR)	IWC, 1982 (Jonsgård and Lyshoel, 1970)
E. North Atlantic	(161)	34.9	(F)	28.9	(P/G of 15 months)	3.5	(1/APR)	IWC, 1982 (Christensen, 1981)
E. North Atlantic	(51)	39.2	(CL)	32.8	(P/G of 15 months)	3.0	(1/APR)	IWC, 1982 (Christensen, 1982)
Antarctic	(91)	27.5	(F)	13.7	(P/G, adj. for season)	7.3	(1/APR)	IWC, 1982 (Mikhalev *et al.*, 1981)
Globicephala melaena								
W. North Atlantic	(500)[1]	39.8	(F)	30.0	(1/S)	3.3	(S)	Sergeant, 1962
E. North Atlantic	(30)	40.0	(F)	—	—	—	—	Purves and Pilleri, 1978
Tursiops truncatus								
Black Sea	(24)	63.0	(—)	63.0	(P/G of 12 months)	1.3–1.5	(1/APR)	Danilevskiy and Tyutyunnikov, 1968
W. North Pacific	(140)	43.6	(F)	43.6	(P/G of 12 months)	—	—	Kasuya and Izumisawa, 1981
Grampus griseus								
W. North Pacific	(13)	30.8	(F)	—	—	—	—	Kasuya and Izumisawa, 1981
Stenella longirostris								
E. trop. Pacific (eastern, 1973–81)	(569)[2]	30.8	(F)	34.9	(P/G of 10.6 months)	2.9	(1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983
E. trop. Pacific (n. whitebelly, 1973–81)	(435)[2]	29.0	(F)	32.8	(P/G of 10.6 months)	3.0	(1/APR)	
E. trop. Pacific (s. whitebelly, 1973–81)	(132)[2]	26.5	(F)	30.0	(P/G of 10.6 months)	3.3	(1/APR)	Perrin and Oliver, 1982
S. coeruleoalba								
E. trop. Pacific (all stocks)	(23)	30.4	(F)	30.4	(P/G of 12 months)	3.3	(1/APR)	Perrin and Oliver, 1982
W. North Pacific (1968–71)	(361)	29.9[4]	(F)	29.9	(P/G of 12 months)	~ 3	(S)	Kasuya, 1972
W. North Pacific (1952–58)	(321)	40.5[4]	(CL)	40.5	(P/G of 12 months)	4.2 (est. initial) to 1.8 (1973)	(1/APR)	Kasuya and Miyazaki, 1975
W. North Pacific (1961–68)	(301)	33.6[4]	(CL)	33.6	(P G of 12 months)			
W. North Pacific (1970–73)	(950)	55.6[4]	(CL)	55.6	(P/G of 12 months)			
W. North Pacific (1971–75)	(165)	70.9[4]	(—)	70.9	(P/G of 12 months)	1.4	(1/APR)	Kasuya, 1976
S. attenuata								
E. trop. Pacific (n. offshore, 1973–78)[3]	(522)[2]	36.0	(F)	37.6	(P/G of 11.5 months)	2.7	(1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982
E. trop. Pacific (n. offshore, 1979–81)	(493)[2]	28.4	(F)	29.6	(P/G of 11.5 months)	3.4	(1/APR)	
E. trop. Pacific (s. offshore, 1973–80)	(277)[2]	39.4	(F)	40.0	(P/G of 11.5 months)	2.5	(1/APR)	Perrin and Oliver, 1982
W. North Pacific (1970–73)	(250)	26.8[4]	(—)	28.7	(P/G of 11.2 months)	3.5	(1/APR)	Kasuya *et al.*, 1974
W. North Pacific (1970–76)	—	—	(—)	25.4[5]	—	3.9	(1/APR)	Kasuya, 1976
Delphinus delphis								
Black Sea (1936–39)	(1179)	—	—	75.0	(I of preg. in 3 out of 4 years)	1.3	(1/APR)	Sleptsov, 1941
Black Sea (1946)	(934)	80.4	(—)	75.0		1.3	(1/APR)	Kleinenberg, 1956
Black Sea (1949)	(231)	40.7	(—)	46.4	(P/G of 11.5 months)	2.2–2.3	(1/APR)	Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	36.2	(F)	37.8	(P/G of 11.5 months)	2.6	(1/APR)	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982

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[1] Excludes 29 'anoestrous or infertile'.

[2] Excludes senescent.

[3] Includes only specimens from sets in which 40 or more killed.

[4] Values differ from those in sources because all PL (simultaneously pregnant and lactating) included here, rather than only ½.

[5] ½ PL included.

of *Delphinus delphis* of 75% reflects a conclusion by Sleptsov (1941) that adult females become pregnant 3 years running and skip the fourth year. The inference was also based on modal progression of fetal and calf length and on regression of ovarian corpora, but mainly on the proportion of pregnant females in the catch. For *Stenella coeruleoalba* in the western North Pacific, Miyazaki and Nishiwaki (1978) have posited similar segregation by reproductive condition and pointed out that the various types of schools have not been equally sampled, causing an overestimate of APR in some studies (e.g. Kasuya and Miyazaki, 1975, and Kasuya, 1976).

For some species, e.g. *S. attenuata* and *S. longirostris*, the range of estimates is fairly small. Where sample size allowed, Henderson, Perrin and Miller (1980) adjusted for bias caused by differential capture vulnerability with age in *S. attenuata* by including data only from purse-seine sets in which 40 or more dolphins were killed; these samples are thought to be more accurately representative of the population than are small-kill samples. The effect is to adjust APR upward. Perrin and Oliver (1982) discussed other biases in the data. The estimates for *S. attenuata* (n. offshore, 1973–78) by the two methods described above (37.6% and 32.3%) are not statistically different from each other (at $\alpha = 0.05$) nor are the estimates of APR for three populations of *S. longirostris* in the eastern tropical Pacific. The 'Method-2' estimates of APR of Perrin *et al.* (1977), Perrin and Henderson (1979) and Henderson *et al.* (1980) are invalid for reasons discussed below in the section on lactation.

The estimate of 13.7% for *Orcinus orca* in the Antarctic (IWC, 1982, from data in Mikhalev, Ivashin, Zavusin and Zelemaya, 1981) is based on division of fetuses into yearly cohorts based on length. This correction is necessary because gestation lasts more than a year and possible because breeding is sharply seasonal.

Length of Lactation and Age at Weaning

The lactation period is the most variable component of the calving cycle. As such, it is important in any model or hypothesis of change in reproductive rate in a population. It can change in two ways: through change in average age at weaning, or through change in differential calf mortality (mortality of nursing calves minus mortality of lactating females). In the former case, the average lactation time per weaned calf decreases with decreased lactation time, but in the latter case it increases (because the lactation time spent on calves that die before weaning must be added to that spent on calves that survive to weaning age).

Estimation methods

(*a*) *Ratio of lactating to pregnant.* The most common method of estimating length of lactation is based on the assumption that the proportion of a sample of mature females that is in a particular reproductive condition is directly proportional to the relative length of time spent in that condition. Thus, if an estimate of length of gestation is available, length of lactation can be estimated as

$$T_L = T_G \cdot L/P$$

where T_G = length of gestation; L = proportion of sample lactating; P = proportion of sample pregnant (including animals both lactating and pregnant). This estimation is based on the same assumptions and subject to the same potential biases as discussed above for the estimation of pregnancy rate.

(*b*) *Cow-calf method.* This method estimates age at weaning. Age at weaning is not equivalent to length of lactation, because it does not take into account differential calf mortality. However, it has often been used as an estimate of lactation time. The cow-calf method assumes that for each lactating cow in a sample there should be also a suckling calf present. The age of the longest calf thus assumed suckling is an estimate of maximum age at weaning. The method assumes that at least some calves reach weaning age. It contains both a downward bias because the longest suckling calf could be expected to continue suckling for some unknown length of time, and an upward bias because it does not consider individual variation in length with age. The method is very sensitive to random error because dispersion of length in the longer calves assumed to be suckling is relatively great and growth at these lengths is relatively slow, meaning that a small difference in length yields a relatively large difference in age estimated from a growth curve.

The cow–calf estimate has been used inappropriately as an estimate of average age at weaning ('Method 2' calculation in Perrin *et al.* (1977) Perrin and Henderson, 1979 and Henderson *et al.* (1980)); the overestimation of lactation time is in addition to that caused by the differential calf mortality (discussed below) that is known to exist in the dolphin population involved in the tuna purse-seine fishery in the eastern tropical Pacific (Perrin and Oliver, 1982). Miyazaki (1977) modified the cow–calf method in an attempt to estimate average weaning age. After assigning calves to suckling or non-suckling categories in each of 19 samples (based on length of the assumed oldest suckling calf in that sample), he used the age at which 50% of all the calves in the pooled sample were estimated to be still suckling as an estimate of average age at weaning. This procedure may improve the accuracy of maximum weaning age as an estimate of length of lactation, but it does not address the problem of differential calf mortality.

In the simplest situation, that of no differential calf mortality (Fig. 4), the accuracy of maximum age at weaning ($w_{\max}$ in Fig. 4a) as an estimate of length of lactation depends on the total length of suckling and on the variance of average weaning age ($\bar{w}$). With the addition of differential calf mortality (in Fig. 4b), lactation can cease in two ways (because of weaning or because of death of the calf with survival of the mother), and weaning age ($w_{\max}$) becomes still more of an overestimate of length of lactation ($\bar{l}$). Sensitivity to amount of differential mortality is high (*B* and *C* in Fig. 4). A countervailing factor causing underestimation of maximum weaning age (by $w_{\max}$ in Fig. 4b) from tuna-fishery data is the fact that too many suckling calves are present in the sample in relation to the number of lactating cows (calves are more vulnerable to capture), causing the length of the longest suckling calf to be underestimated. In the extreme case of complete differential mortality, i.e. no survival to weaning age (*D* in Fig. 4), the estimate of weaning age by the cow–calf method becomes actually an estimate of maximum length of lactation corresponding to maximum age to which

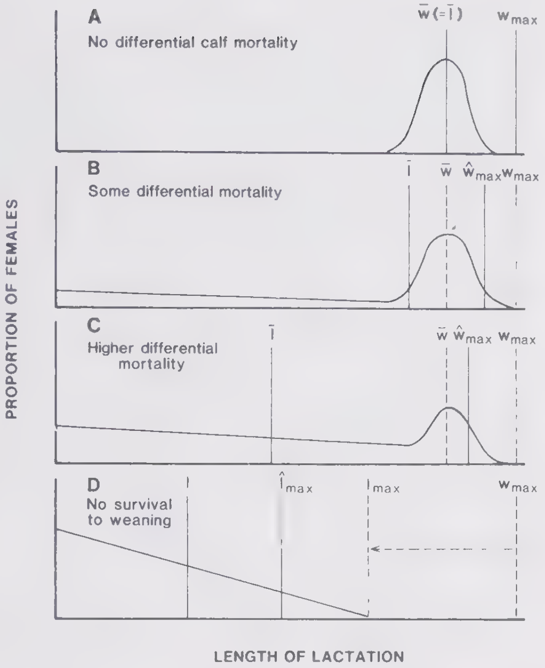

Fig. 4. Conceptual model of relationships between length of lactation (l), age at weaning (w) and differential calf mortality.

calves survive (l_{max}). The complete relationships between estimates of weaning, estimates of length of lactation and differential calf mortality have not been quantitatively modeled, so the usefulness of the cow–calf method at this point is problematical.

(*c*) *Stomach contents*. Although the examination of stomach contents allows direct determination of a shift from milk to solid food plus milk, (e.g. Perrin *et al*., 1976) estimation of age at weaning by this method is open to question because of the difficulty of detecting small quantities of milk mixed with solid food. Odontocetes may continue to suckle for long periods, in some cases years after a major shift to solid food. The extended duration of cow–calf bonding may serve some non-nutritional function (Brodie, 1969). P. B. Best (personal communication to WFP) has employed a chemical test for lactose in his examination of sperm-whale stomachs. The color reagent used can detect sperm-whale milk at a 30-fold dilution. Without data on suckling rates and milk volume consumed during the latter stages of nursing lasting for years and data on the rate of digestion of milk, it is not possible to know whether this test is sufficiently sensitive to allow estimation of weaning age from stomach contents.

If mortality rates for weaned and unweaned calves are different, an estimate of average age at weaning based on a 50%-weaned criterion for a sample of animals would be biased. For example, if weaned calves have higher mortality, the estimate of average weaning age would be biased upward.

(*d*) *Behavioral observations*. Individual nursing calves can be observed in captivity or in the wild. This method has resulted in a general concensus that *Tursiops truncatus* calves usually nurse about 18 months, with a lot of variation. For other species that are rare in captivity or difficult to observe in the wild, a sample-size problem is soon encountered. There is also the question of the effect of captivity. A bottlenose dolphin in an oceanarium in South Africa developed a habit of squirting milk at the glass at an observation post to startle visitors. This animal suckled for 38 months, possibly because of the learned behavior (Ross, 1979).

Available estimates

The available estimates of length of lactation (Table 7) range from 8 months (*Stenella coeruleoalba* off Japan during the period 1970–73) to 27 months (*S. attenuata* off Japan, 1970–76). The modal value appears to be 18–20 months (8 of the 21 estimates in Table 7). The relatively low values for *S. coeruleoalba* off Japan (8–20 months) and *Delphinus delphis* in the Black Sea (14–19 months) reflect the segregation of calving females discussed above for both cases. The possible effects of exploitation on length of lactation (thought to have operated, for example in the western Pacific population of *S. coeruleoalba* and the eastern Pacific populations of *S. longirostris*) are discussed below in the section on the topic.

The range of estimates of age at weaning is greater (5 months to 34 months) than for length of lactation. The lowest value of 5–6 months for *D. delphis* in the Black Sea again reflects segregation of lactating females. The estimates of weaning age for the three populations of *S. longirostris* (11, 19 and 34 months) are inversely correlated with the three estimates of length of lactation (19, 18 and 15 months); this inconsistency is discussed below in the section on effects of exploitation.

Solid food is taken in the first year of life in delphinids; the six estimates range from 3–6 months to 4–11 months with the mean at about 6 months. Maximum length of suckling is at least 2 years; the six estimates range from 24 months to 48–60 months.

Length of 'Resting Period'

In estimating reproductive rates, mature females are usually classified into four categories: pregnant only (P), pregnant and lactating (PL), lactating only (L) and 'resting' (R) (all those neither pregnant nor lactating). In some analyses, e.g. Perrin *et al.* (1976), Perrin *et al.* (1977) and Henderson *et al.* (1980), senescent females (those neither pregnant nor lactating and with small withered ovaries containing no recent corpora) were not included in the resting category. In most studies, the category is a catchall and includes females in estrus, those between ovulation cycles, senescent females, those that have recently aborted and those pregnant with very small embryos missed in dissection. The length of the 'resting' period is calculated in the same manner and is subject to the same potential biases as the estimates of length of lactation or length of gestation:

$$T_R = T_G \cdot R/P$$

where T_G = gestation time, R = proportion resting and P = proportion pregnant.

In alternative estimates of annual pregnancy rates based on independent estimates of gestation and weaning age (the 'Method 2' estimates of Perrin *et al.* (1977)

Table 7

Estimates of length of lactation, age at weaning and length of 'resting period' in delphinids. Methods noted: observed in wild, observed in captivity, determined from stomach contents, determined from eruption of teeth, estimated by cow–calf method (C–C), estimated from ratio of lactating to pregnant (L/P) and estimated from ratio of 'resting' to pregnant

	LACTATION		WEANING							
Species and region (stock or year in parentheses)	Mature females (no.)	Length (by L/P) (months)	Age at first solid food (months)	(Method)	Oldest nursing (months)	(Method)	Average age at weaning (months)	(Method)	'Resting' (by R/L) (months)	Source of estimate or data
Pseudorca crassidens										
W. North Pacific	(38)	18¹	—	—	—	—	—	—	—	Kasuya and Izumisawa, 1981
Orcinus orca										
E. North Pacific	—	—	—	—	—	—	⩾ 12	(ob. wild)	—	IWC, 1982
Globicephala melaena										
E. North Atlantic	(485)	22	6–9	(stom.)	—	—	—	—	8	Sergeant, 1962
Lagenorhynchus acutus										
E. North Atlantic	(32)	18²	—	—	—	—	—	—	—	Sergeant *et al.*, 1980
Tursiops truncatus										
All regions	(31)	19³	4–11	(ob. cap.)	38	(ob. cap. and wild)	18–20	(ob. cap. and wild)	5	Kasuya and Izumisawa, 1981; Leatherwood *et al.*, 1978; McBride and Kritzler, 1951; Prescott, 1977; Ridgway and Benirschke, 1977; Ross, 1977, 1979, Saayman and Taylor, 1977; Sergeant, 1962
Stenella longirostris										
E. trop. Pacific (eastern, 1973–81)	(569)	19	—	—	—	—	11⁴	(C–C)	6	Henderson *et al.*, 1980;
E. trop. Pacific (n. whitebelly, 1973–81)	(435)	18	—	—	—	—	19⁴	(C–C)	9	Oliver *et al.*, 1983;
E. trop. Pacific (s. whitebelly, 1973–81)	(132)	15	—	—	—	—	34⁴	(C–C)	15	Perrin and Oliver, 1982
S. coeruleoalba										
E. trop. Pacific (all stocks)	(28)	14³	—	—	—	—	—	—	10	Perrin and Oliver, 1982
W. North Pacific (1968–71)	(361)	12³	~ 6	(erupt. teeth)	24	(—)	⩾ 15	(C–C)	5	Kasuya, 1972
W. North Pacific (1952–58)	(321)	17³	—	—	—	—	—	—	4	Kasuya and Miyazaki, 1975
W. North Pacific (1961–68)	(301)	20³	—	—	—	—	—	—	5	Kasuya and Miyazaki, 1975
W. North Pacific (1970–73)	(950)	8³	—	—	—	—	—	—	2	Kasuya and Miyazaki, 1975
W. North Pacific (1971–75)	(—)	13³	—	—	~ 36	(—)	—	—	4	Kasuya, 1976
W. North Pacific (1972–73)	—	—	3–6	(stom.)	36	(C–C)	18	(C–C)⁵	—	Miyazaki, 1977
S. attenuata										
E. trop. Pacific (n. offshore, 1973–78)	(522)⁶	17	5–7	(stom.)	33	(C–C)	20	(C–C)	5	Henderson *et al.*, 1980;
E. trop. Pacific (n. offshore, 1979–81)	(493)	26	—	—	—	—	—	—	6	Oliver *et al.*, 1983;
E. trop. Pacific (s. offshore, 1973–80)	(277)	13	—	—	—	—	—	—	5	Perrin *et al.*, 1976; Perrin and Oliver, 1982
W. North Pacific (1970–73)	(250)	26	3–6	(stom.)	48–60	(C–C)	—	—	7	Kasuya *et al.*, 1974
W. North Pacific (1970–76)	(—)	27	—	—	—	—	—	—	9	Kasuya, 1976
Delphinus delphis										
Black Sea (1931–33)	(~ 800)	14⁷	—	—	—	—	—	—	—	Mayarova and Danilevskiy, 1934
Black Sea (1936–39)	—	—	—	—	—	—	5–6⁸	(—)	—	Sleptsov, 1941
Black Sea (1946)	(934)	—	—	—	—	—	6⁸	(—)	—	Kleinenberg, 1956
Black Sea (1949)	(231)	19⁷	—	—	—	—	—	—	4	Sokolov, 1962
E. trop. Pacific (all stocks)	(365)	19⁷	—	—	—	—	—	—	4	Henderson *et al.*, 1980; Oliver *et al.*, 1983; Perrin and Oliver, 1982

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[1] Assumed gestation of 16 months.

[2] Assumed gestation of 11 months.

[3] Assumed gestation of 12 months.

[4] For 1973–78 only ($n = 521$, 366 and 123).

[5] Modified as described in text.

[6] Includes only specimens from net hauls in which 40 or more were killed (see text, under *Pregnancy rate*).

[7] Assumed gestation of 11.5 months.

[8] But see text.

and Henderson *et al.* (1980)), *R/P* estimates of length of the 'resting' portion of the calving cycle were used.

The available estimates (Table 7) range from 2 months (for the reportedly depleted population of *S. coeruleoalba* off Japan) to 15 months (for the southern whitebelly population of *S. longirostris* in the eastern tropical Pacific). The modal value is 4–5 months (9 of the 18 estimates).

Age and Sex Structure

Background and methods

Sex ratios and age structure are usually estimated from series of specimens captured in fisheries or collected from strandings. Rather than follow a single age class throughout its life (which has not been possible for delphinids) to determine sex ratios, age structures and mortality/survival rates, the usual method is to estimate these parameters using a sample from one time period. These techniques are adapted from human demography and fisheries and wildlife sciences (e.g. Keyfitz, 1968; Ricker, 1975; Caughley, 1977).

Assumptions involved in making sex- and age-structure inferences from specimen series include (1) age and sex are accurately determined; (2) the sample is representative of the population; and (3) the population is stationary in structure. The difficulty of testing these assumptions increases in the order in which they are listed.

Sex is more easily determined than age for dead specimens, and estimates of sex ratio are therefore generally more reliable than those of age structure. Both sex and age are often very difficult to determine for live specimens in studies that do not involve capture. Species with marked sexual dimorphism (e.g. *O. orca*) are exceptions to this, at least for sex ratio of adults.

Recent developments in age determination are reviewed in Perrin and Myrick (1980). In some cases, ovarian-corpora frequencies have been used to represent age in adult females on the assumption that ovulation is a regular event. Since this assumption is probably not valid (see discussion above), age estimates from corpus frequencies are not reliable.

While it is probably not possible to determine with a great deal of certainty that an observed age series is representative of the population, some simple methods can identify strongly biased samples. For example, there should in general be fewer individuals in older age classes. Distributions which have peak frequencies at ages over 0–1 indicate under-representation of juveniles. This type of age distribution has been observed for many delphinid populations (see below).

To date, stationarity has not been demonstrated for any delphinid population. Again, this would in fact be very difficult to do. Any information suggesting recent changes in overall population size would invalidate this assumption.

Common methods used to estimate adult mortality rates in fisheries and wildlife sciences include log-linear regression (e.g. Ricker, 1975) and the Chapman–Robson (1960) method. Regression methods were used by Kasuya *et al.* (1974) and Kasuya (1976) for *S. attenuata*, and by Sergeant (1962) for *G. melaena*. In some instances it is possible to factor out influences from population growth and mortality via exploitation from the total mortality represented by an observed age structure (e.g. see Ohsumi, 1979).

Available estimates

In every case for which data exist on sex and age structure of a delphinid population, two patterns have surfaced. First, the ratio of males to females appears to decline with age (Table 8). Second, a certain segment of the population, roughly 'juvenile' in age, appears to be under-represented in the samples. This second observation suggests that any reproductive parameter estimated from relative frequencies of age classes (mortality rate, ages at sexual maturity and first birth, relative pregnancy by age) may be biased. In some cases there are also sex differences in the under-representation of juveniles, e.g. in *Stenella attenuata* of the eastern tropical Pacific (J. Barlow, A. Hohn and A. Myrick, pers. comm. to SBR), *Globicephala melaena* near Newfoundland (Sergeant, 1962), and *Stenella coeruleoalba*, near Japan (Miyazaki and Nishiwaki, 1978).

A wide range in sex ratios for entire populations has been reported (Table 8): from 5.5:1 for *Lagenorhynchus acutus* in Norway down to 0.5:1 for *Tursiops truncatus* off North Carolina (Townsend, 1914). Within the Black-Sea *Delphinus* data alone, the range is from 0.64:1 to 2.85:1, depending upon the month during which the nearshore schools were captured. This variation is most likely due in great part to age/sex segregation, which has been shown to be seasonal in the Black Sea (Kleinenberg, 1956; Tomilin, 1957; Mayarova and Danilevskiy, 1934). The same is true for *Tursiops truncatus* off the eastern US (True, 1891). Segregation by sex and/or age has been observed both within and between groups in studies of free-ranging *Tursiops truncatus* (Lear and Bryden, 1980; Wells, Irvine and Scott 1980; Würsig, 1978), *Stenella longirostris* (Norris and Dohl, 1980a; Pryor and Kang, 1980), *Stenella attenuata* (Pryor and Kang, 1980), *Sousa* sp. (Saayman and Tayler, 1979), *Lagenorhynchus obliquidens* (Norris and Prescott, 1961), *L. obscurus* (Würsig and Würsig, 1980) and *Orcinus orca* (Bigg, 1982; Balcomb, Boran and Heimlich, 1982; Condy, van Arde and Bester, 1978). Age/sex segregation has been reported from studies of captured schools for *Stenella attenuata* (Kasuya, 1976; Kasuya *et al.*, 1974) *S. coeruleoalba* (Kasuya, 1972, 1976; Miyazaki and Nishiwaki, 1979), *Delphinus delphis* (Mayarova and Danilevskiy, 1934; Kleinenberg, 1956; Tomilin, 1957; Hui, 1973), *Tursiops truncatus* (True, 1891; Mead, 1975b), *Lagenorhynchus acutus* (St Aubin and Geraci, 1979) and *Globicephala melaena* (Sergeant, 1962). The implications of age and asexual segregation on estimating delphinid population parameters are profound. As discussed above, unbiased estimation of many vital rates requires representative age-structure samples. Since age and/or sex segregation may be the rule rather than the exception for delphinids, data should be scrutinized closely before calculation of vital-rate statistics.

Estimates of natural mortality have been made for only three delphinid cetaceans: *G. melaena* (0.115: Sergeant, 1962), *S. coeruleoalba* (0.137: Kasuya, 1976) and *S. attenuata* (0.161: Kasuya, 1976), as reviewed and evaluated by Ohsumi (1979). In each case the original authors made more than one estimate. Values reported

(continued on p. 114)

Table 8

Sex ratios reported for delphinids, listed here as ♂:♀, with female values scaled to 1.0. Data from studies which selected by sex are not listed here

Species and region	Data type	Age class and sample size	♂:♀ ratio	Age class and sample	♂:♀ ratio	Age	♂:♀ ratio	Source
Orcinus orca								
(Pacific N.W., U.S.)	Live observation	Adult (43)	0.48:1	—	—	—	—	Balcomb *et al.*, 1982
(Pacific N.W., U.S.)	Live observation	Adult (132)	0.83:1	—	—	—	—	Bigg, 1982
(Marion Island)	Live observation	Adult (478)	1.34:1	—	—	—	—	Condy *et al.*, 1978
Globicephala macrorhynchus								
(Florida)	Mass stranding	All (135)	0.53:1	—	—	—	—	Irvine *et al.*, 1979
(California)	Mass stranding	All (27)	0.28:1	—	—	—	—	Hall *et al.*, 1971
G. melaena								
(Nova Scotia)	Mass standing	All (99)	1.91:1	—	—	—	—	Geraci and St. Aubin, 1977
(Newfoundland)	Drive fishery	Newborn (250)	1.43:1	6–10 years (87)	0.85:1	8–22 years (213)	0.32:1	Sergeant, 1962
Pseudorca crassidens								
(Scotland)	Mass stranding	All (72)	0.85:1	—	—	—	—	Purves and Pilleri, 1978
(Scotland)	Mass stranding	All (62)	0.82:1	—	—	—	—	Peacock *et al.*, 1936
Feresa attenuata								
(Japan)		All (14)	1:1	—	—	—	—	Nishiwaki *et al.*, 1956
Steno bredanensis								
(Florida)	Mass stranding	All (10)	1.5:1	—	—	—	—	Layne, 1965
Lagenorhynchus acutus								
(New England)	Mass stranding	'Young' (16)	1.67:1	'Intermed.' (30)	1.72:1	'Adult' (56)	0.22:1	Sergeant *et al.*, 1980
(Norway)		All (22)	5.5:1	—	—	—	—	Guldberg and Nansen, 1894
Tursiops truncatus								
(N. Carolina)	Drive fishery	All (157)	1.14:1	—	—	—	—	True, 1890
(Florida)	Live capture	All (61)	1:1	—	—	—	—	Sergeant *et al.*, 1973
(Florida)	Live capture	All (47)	0.96:1	—	—	—	—	Irvine *et al.*, 1981
(N. Carolina)	Drive fishery	All (51)	0.5:1	—	—	—	—	Townsend, 1914
(Black Sea)	Drive fishery	All (53)	1:1	—	—	—	—	Danileyskiy and Tyutyunnikov, 1968
Stenella longirostris								
(Florida)	Mass stranding	All (25)	0.85:1	—	—	—	—	Mead *et al.*, 1980
(ETP: 1973–75)	Tuna seine	— (294)	1.1:1	1.3–1.6 m (631)	0.99:1	Adult (1,330)	0.94:1	Perrin *et al.*, 1976
(ETP: 1979–80)	Tuna seine	All (734)	0.98:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (305)	1.15:1	—	—	—	—	Oliver *et al.*, 1983
S. attenuata								
(ETP)	Tuna seine	Neonate (412)	1:1	'2-tone' (1,367)	0.95:1	'Speckled' (1,275)	0.91:1	Perrin *et al.*, 1976
		Mottled (1,298)	0.73:1	'Fused' (5,019)	0.75:1	—	—	Perrin *et al.*, 1976
(ETP: 1976)	Tuna seine	All (6,225)	0.8:1	—	—	—	—	Perrin *et al.*, 1977
(ETP: 1979–80)	Tuna seine	All (2,246)	0.75:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (830)	0.73:1	—	—	—	—	Oliver *et al.*, 1983
(Japan)	Drive and harpoon fishery	Juv. (149)	1.16:1	'Puberal' (167)	2.21:1	'Mature' (422)	0.38:1	Kasuya *et al.*, 1974

Table 8 (*continued*)

S coeruleoalba								
(Japan)	Drive and harpoon	Juv. school (276)	3.07:1	Mixed school (653)	1.06:1	Adult school (1,638)	0.78:1	Miyazaki and Nishiwaki, 1978
(Japan)	Drive and harpoon	Fetus (661)	1.13:1	'Suckling' (744)	1.07:1	Others (7,967)	1.19:1	Kasuya and Miyazaki, 1975
(Japan)	Drive and harpoon	0–1.5 year (251) 14.5+year (747)	1.09:1 0.77:1	2.5–8.5 years (1,438)	1.55:1	9.5–13.5 years (847)	0.93:1	Miyazaki, 1977
(Japan)	Drive and harpoon	'Prenatal' (115)	1:1	'Postnatal' (1,048)	0.73:1	—	—	Miyazaki, 1977
Delphinus delphis								
(ETP: 1973–78)	Tuna seine	All (140)	0.95:1	—	—	—	—	Henderson *et al.*, 1980
(ETP: 1979–80)	Tuna seine	All (363)	0.85:1	—	—	—	—	Perrin and Oliver, 1982
(ETP: 1981)	Tuna seine	All (117)	1.05:1	—	—	—	—	Oliver *et al.*, 1983
(Black Sea: 1930s)	Drive fishery	All (82, 843)	1.12:1	—	—	—	—	Tomilin, 1957
(ETP: north)	Tuna seine	All (286)	0.87:1	—	—	—	—	Hui, 1977
(ETP: south)	Tuna seine	All (799)	0.85:1	—	—	—	—	Hui, 1977
(Black Sea: 1931)	Drive-or-gun fishery	All (395)	1.5:1	—	—	—	—	Danilevskiy and Tyutyunnikov, 1968
(Black Sea: 1931, Jan.)	Drive-or-gun fishery	All (212)	0.64:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Feb.)	Drive-or-gun fishery	All (176)	2.85:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Mar.)	Drive-or-gun fishery	All (589)	1.44:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Apr.)	Drive-or-gun fishery	All (687)	1.56:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, May)	Drive-or-gun fishery	All (277)	2.12:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Jul.)	Drive-or-gun fishery	All (384)	1.56:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Aug.)	Drive-or-gun fishery	All (440)	1.17:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(Black Sea: 1931, Sept.)	Drive-or-gun fishery	All (135)	0.69:1	—	—	—	—	Mayarova and Danilevskiy, 1934
(So. Calif: 1971)	Tuna seine	0–4 (68)	—	5–10 (28)	0.70:1	11+(19)	0.9:1	Hui, 1973
(ETP: 1977)	Tuna seine			—	—	—	—	Gurevich and Stewart, 1978

Table 9

Annual birth rates reported for populations of delphinids

Species and region/stock	b or GARR	Notes	Source
Sousa chinensis			
Indian Ocean	0.10(b)	Visual obs. % calves in population	Saayman and Tayler, 1979
Orcinus orca			
Puget Sound, WA.	0.04–0.05	Visually obs. preg. rate × % female adult	Dahlheim, 1980
Vancouver Is., B.C.	0.046(b)	No. calves/no. all others ('cropped' population)	IWC, 1982
Vancouver Is., B.C.	0.032	'Uncropped' state	IWC, 1982
Puget Sound, WA.	0.026(b)	Obs. no. calves/no. all others	IWC, 1982
Globicephala melaena			
Newfoundland	0.132	% female × % mature female preg. divided by gestation (exploited)	Sergeant, 1962 Harrison, 1969
Tursiops truncatus			
Florida	0.082(b)	% calves visually counted (non-exploited)	Irvine *et al.*, 1981
N. Gulf of Mexico	0.077(b)	% calves visually counted (exploited)	Leatherwood, 1977
Argentina, S. Atlantic	0.096(b)	% calves visually counted (non-exploited)	Würsig, 1978
E. Australia	0.012(b)	% calves visually counted (non-exploited)	Lear and Bryden, 1980
Black Sea	0.30?	% female × % female mature × % preg. (biased sampling suspected) (exploited)	Danilevskiy and Tyutyunnikov, 1968
Stenella longirostris			
Eastern stock, ETP	0.08	% female × % female mature × % preg. (exploited)	Perrin *et al.*, 1977
	0.075	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Northern whitebelly stock, ETP	0.094	% female × % female mature × % preg. (exploited)	Perrin and Henderson, 1984
Southern whitebelly stock, ETP	0.067	% female × % female mature × % preg. (exploited)	Henderson *et al.*, 1980
Stenella coeruleoalba			
All stocks, ETP	0.109	% female × % female mature × % preg. (exploited)	Henderson *et al.*, 1980
Japan	0.11	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1972
Japan	0.103	% female × % mature × % preg. (exploited) (calculation from data given)	Kasuya, 1976
Stenella attenuata			
Japan	0.103	% female × % mature × % preg. (exploited) (calculated from data in both papers)	Kasuya, 1976 and Kasuya *et al.*, 1974
Northern offshore stock, ETP	0.117	% female × % mature × % preg. (exploited) (calculated from data in both papers); 1973-1978 data	Henderson *et al.*, 1980
Northern offshore stock, ETP	0.109	% female × % mature × % preg. (exploited); 1973–1975 data	Perrin *et al.*, 1977
Southern offshore stock, ETP	(0.195)	(M1)	Henderson *et al.*, 1980
Delphinus delphis			
ETP	0.096	(Exploited) (M1)	Henderson *et al.*, 1980
Northern stock, E. Pac.	0.087	No. preg./total population	Hui, 1977
Southern stock, ETP	0.066	No. preg./total population	Hui, 1977
Black Sea	0.106[1]	% all female preg. × % female (exploited)	Danilevskiy and Tyutyunnikov, 1968

[1] Adjusted for 10-month gestation $= (12/10) \times (22/35) \times 0.35 \times 0.4 = 0.106$. Unadjusted $= 0.22 \times 0.4 = 0.088$.

here are those which Ohsumi (1979) concluded to be the most appropriate. All of these estimates are tentative, incorporating unresolved problems in age determination and possibly sampling biases. Direct observations of *O. orca* in Puget Sound indicated a relatively low adult natural mortality rate of $M = 0.01$ (Balcomb *et al.*, 1982).

Ohsumi (1979) and Ralls, Brownell and Ballou (1980) have reviewed the available data on mortality rates for delphinid cetaceans (among other taxa). Ralls *et al.* found that the degree to which males have higher mortality increases with the degree of sexual dimorphism. Ohsumi (1979) investigated the relationships between M, life span and asymptotic body size. He found that, in general, larger, longer-lived taxa have lower natural mortality rates. Since his data included mysticete as well as odontocete species, it is not clear how accurate his predictions of M would be for species not included in the original analysis.

Reproductive Rates

There are two types of population reproductive rates of interest in stock assessment and management. These can be generally categorized as gross and net rates, differing roughly by annual natural mortality. Each category encompasses a number of specific types of estimates and each has been addressed in more than one way. These are summary parameters, usually estimated from combina-

Table 10

Net annual reproductive rates reported for delphinids

Species and region	Net repro. rate	Notes	Source
Orcinus orca			
Vancouver Is., B.C.	0.031	Observed net pod change 'cropped' state	IWC, 1982
Vancouver Is., B.C.	0.017	Observed net pod change 'uncropped' state	IWC, 1982
Puget Sound, WA	0.023	Observed net pod change 'cropped' state	IWC, 1982
Stenella coeruleoalba			
Japan	0.031–0.032	Computed in complex manner, observed F, assumed M, est. N, CI, sex ratio	Kasuya and Miyazaki, 1975
Japan	0.023–0.024	Above data re-evaluated from new age determinations and catch data	Kasuya, 1976
Japan	0.044	'Intrinsic' rate, extrapolated from series of r_t, N_t	Kasuya, 1976

tions of other, directly measured (or assumed) statistics. It is generally assumed that one or both categories vary in a density-dependent manner such that net reproduction increases as density decreases from the so-called carrying capacity level. Such a change in net reproduction was estimated to have occurred for *Stenella coeruleoalba* near Japan (Kasuya, 1976).

The general category of 'gross' rates (Table 9) includes estimates of crude birth rates (b) (Keyfitz, 1977) and gross annual reproductive rates (GARR) (Perrin *et al.*, 1976; Smith, 1983). Ideally the crude birth rate is estimated as $b = \int_{x=0}^{\infty} c_x m_x dx$, where m_x is the probability that a female aged x will give birth during each time period, and c_x is the proportion of the population composed of mature females aged x (Keyfitz, 1977). In practice the crude birth rate has been calculated as the estimated number of newborn calves divided by the estimated total population (e.g. Saayman and Taylor, 1977; Leatherwood, 1977, Würsig, 1978). This is usually a biased estimate since (1) it doesn't consider calf mortality from birth to the census time; (2) calving is usually diffusely seasonal and some births may take place after the census; and (3) cow mortality is not considered. The degree of inaccuracy is related to the degree of calving seasonality, the timing of the census in relation to the calving pulse, and the differentials in mortality between newborn calves, reproductive females and the rest of the population. The most accurate estimate of this type would be made from a census taken just following the completion of a very sharply-defined annual calving period. Even then it would be an overestimate, not considering cow mortality during the previous time period. (Such mortality is implicitly considered in the 'ideal' formulation given above).

The other type of gross rate, 'GARR', is usually estimated as the product of the proportion of the population that is female, the proportion of females sexually mature and the annual pregnancy rate (APR). GARR has been shown to be very sensitive to the method of estimation of APR (Perrin and Henderson, 1984; Henderson *et al.*, 1980). Estimation of GARR by the product method also requires the assumption of unbiased estimates of sex ratio and the proportion of females which are sexually mature; it is therefore sensitive to problems in estimating these parameters (as discussed above). However, GARR can also (more simply) be estimated as the proportion of pregnant females in the total population, with adjustment for length of gestation. While subject to some of the same assumptions this method is more straightforward than the product method.

The 'Method-2' estimates of GARR of Perrin *et al.* (1977) are invalid for reasons discussed above in the section on lactation.

GARR and the crude birth rate differ in that the latter includes integration of mortality of cows while GARR does not. Both statistics can be useful indices of relative population status. Especially with GARR, within-population comparisons over time are more informative than between-population comparisons. Polacheck (1982) has shown that age-structure effects alone can confound between-population comparisons of GARR estimates, obscuring any looked-for trend in GARR with population level (e.g. see Perrin and Henderson, 1984).

Net reproductive rates represent reproduction in excess of mortality for a population as a whole. They are extremely difficult to obtain for cetaceans, as demonstrated by the paucity of points in Table 10. In the strict context of human demography, the term 'net reproduction' refers to R_0, which is the number of female offspring expected to be born to a female given existing rates of age-specific survival and reproduction (Keyfitz, 1977). In practice, for delphinids, the more general definition given above is usually the one used. One method of estimating net reproduction which has been considered is the subtraction of population natural mortality from GARR (Smith, 1983). This is incorrect, as the natural mortality should be subtracted from crude birth rate to estimate net increase. Unfortunately, natural mortality is also very difficult to measure and (in the case of *Stenella* spp.) must be assumed from comparison with other populations. In this case, the GARR of an assumedly unexploited stock has been taken as equivalent to natural mortality for that stock. This second GARR has then been subtracted from that for the exploited population. This systematically overestimates net recruitment for the exploited population (personal communication to SBR from D. Goodman).

The most accurate way to measure net reproduction is to observe net changes in total population size in the absence of (or concomitant with a known level of) removals by humans. So far this has been feasible only for small groups of killer whales in the Pacific Northwest in which nearly all individuals are identifiable (Table 10).

Another method which has been employed to estimate net reproduction of a delphinid population is that utilized by Kasuya (1976) and Kasuya and Miyazaki (1975) for *Stenella coeruleoalba* off Japan. Theirs is a fairly complex series of computations which is based upon observed fishing mortality, estimated sex ratio, age structure, population size and an assumed natural mortality rate (i.e. a version of GARR – M, which doesn't explicitly compute GARR enroute).

No variances are listed for gross or net rates in Tables 9 or 10. This is because they were usually not reported in the source literature. It would be possible to derive and compute them in most cases. The ranges reported (0.026–0.144 gross and 0.017–0.032 net) reflect different estimation methods and different amounts and quality of data and represent populations in a variety of states: heavily, lightly or not exploited. Consequently it is not appropriate to draw any general inferences from the ranges except perhaps as indications of reasonable limits for these parameters.

DISCUSSION

Effects of Seasonality

Seasonality of mating and calving has been demonstrated for all delphinids that have been studied in any depth, although the degree of seasonality (intensity of breeding peaks) varies greatly. The impact of seasonality on estimating parameters depends on the degree of seasonality (Fig. 5) and also on the length of gestation and lactation. For example, if pregnancy and lactation each last about a year and breeding peaks are moderately diffuse (as in *S. attenuata* in the eastern Pacific – Perrin *et al.*, 1976), seasonality can be expected to have negligible effect on estimates of reproductive parameters. On the other hand, if pregnancy lasts about a year and a third (as in the pilot whales and the killer whale – Table 2), even moderate seasonality can lead to considerable bias in estimates. Barlow (1984) discusses the nature and impact of seasonal bias.

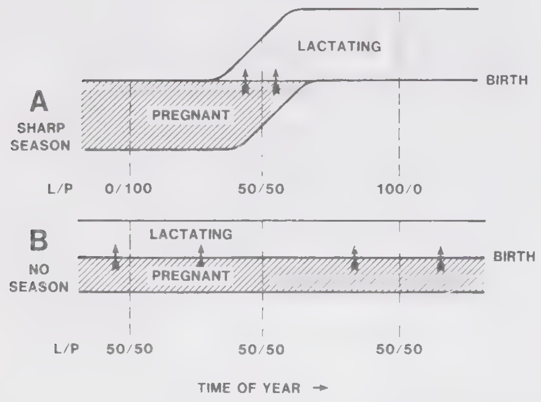

Fig. 5. Effect of sharp breeding seasonality on estimates of pregnancy and lactation. A hypothetical extreme case in which pregnancy and lactation each last six months.

Effects of Schooling Segregation

Estimates of reproductive parameters based on samples from a catch assume that the samples accurately represent the population at large in terms of age, sex and reproductive condition, and initial population studies of several delphinids relied on this assumption (*Delphinus delphis* – Mayarova and Danilevskiy, 1934; Sleptsov, 1941; *Stenella coeruleoalba* – Kasuya, 1972; *S. attenuata* and *S. longirostris* – Perrin *et al.*, 1976 and 1977, Perrin and Henderson, 1984; Henderson *et al.*, 1980). More recent work, however, has indicated that schooling segregation of one sort or another may be a general feature of delphinid life history and must be taken into account in estimating reproductive parameters (Norris and Dohl, 1980a and b; Würsig and Würsig, 1980; Miyazaki and Nishiwaki, 1978). As discussed above, Kleinenberg (1956) discovered that female common dolphins, *D. delphis*, in the Black Sea to some extent school separately during calving and early lactation in an offshore area not usually involved in the dolphin fishery, leading to erroneously high estimates of pregnancy rate and low estimates of length of lactation based on samples of the catch. The estimate of the length of the calving cycle is now about twice the earlier estimates, about 2 years rather than about 1 year (Sokolov, 1962), a difference obviously of great import to assessment and management. The most recent parameter estimates for *S. coeruleoalba* off Japan (Miyazaki, 1984; Kasuya, 1984) take into account the now-well-documented existence of several kinds of schools that are sampled differentially by the fishery (Miyazaki and Nishiwaki, 1978). The most recent information on age structure of the northern offshore population of *S. attenuata* in the eastern Pacific (personal communication, A. A. Hohn, A. C. Myrick, Jr. and J. Barlow) indicates that a substantial portion of females just at or below the average age at attainment of sexual maturity are not represented in the samples of dolphins killed incidentally in the tuna fishery and probably school separately in schools that for some reason are not associated with tuna, throwing all the published estimates of reproductive parameters in the population (cited above) into question.

Clearly schooling segregation is possibly a general phenomenon in delphinids, and it should not be assumed to not exist or not be of importance in any population. In some cases, the sampling problems caused by it may be insoluble but they cannot be denied.

Effects of Geographical Variation

As can be seen in the various tables and in the appendices to this report, estimates of life-history parameters often vary sharply between populations of the same species. Several reasons for this are possible:

(1) Sample sizes were inadequate, and the differences are ascribable to statistical error.

(2) The samples were biased in one case or the other and were not accurately representative of the population(s).

(3) Different analytical methods were used to arrive at the estimates.

(4) The differences reflect real differences in the status

of the populations, e.g. change in carrying capacity or density (discussed in next section).

(5) The differences are real and inherent, i.e. genetically determined geographical variation.

For dynamic parameters such as age at attainment of sexual maturity, pregnancy rate and length of lactation, it is difficult or impossible to determine whether reasons 2, 4, or 5 are responsible for differences in estimates. For example, the differences between estimates for *Stenella attenuata* in the eastern Pacific and the western Pacific (Tables 4, 6 and 7) could be due to differential bias known to exist (but not measured – Perrin and Oliver, 1982; Miyazaki, 1977) in the two kinds of fisheries involved, to the differential status *vis-a-vis* exploitation (Smith, 1983) or, at least partially, to inherent differences in basic life-history features. It is interesting to note, however, that where problems of sampling bias are thought to be uniform and analytical methodologies are the same for two or more populations of the same species, e.g. *S. attenuata* and *S. longirostris* in the eastern Pacific, differences in most or all estimates of dynamic parameters are statistically insignificant.

Some parameters, such as maximum size and average size of adults, vary geographically independent of dynamic factors. *Tursiops truncatus* is a notable example. The range of variation in adult length (Appendix 1) is enormous, from 202 cm for the smallest female to 381 cm for the largest male, nearly a two-fold difference. The sample sizes for adult female bottlenose dolphins from two regions, Florida and the western North Pacific (Appendix 3), are sufficiently large to allow determination that the difference in average length (239 cm vs 288 cm) is real ($P < 0.001$). The differences in maximum size, length of largest immature and length of smallest mature animals (Appendix 1) between samples from several other regions suggest that there are probably real differences among them as well (eastern North Atlantic, Black Sea, western North Atlantic, Gulf of Mexico, eastern North Pacific, and Indian Ocean – the '*aduncus*' form). This pattern of wide geographical variation in the best-known delphinids and similar patterns in other species for which large volumes of data have been available for two or more regions (e.g. *Stenella longirostris*, and *Delphinus delphis*, Appendices 1 and 3) suggest that considerable geographical variation in size is to be expected in any broadly distributed small cetacean and should be taken into account in any deductive modeling of relationships among parameters (discussed below).

Effects of Exploitation

Population and management models that incorporate the concept of net production (sustainable yield available for harvest, or population growth increment) are based on the assumption that reproductive rates and/or natural mortality rates change with population density (Perrin and Donovan, 1984; Smith, 1983). The reproductive parameter estimates tabulated here can be examined for correlation with population status (present size/pre-exploitation size). The species for which large amounts of data exist for one population through time (or for more than one population of the same species for which the analytical methods are the same) and any sampling biases can be expected to be the same, are *Stenella longirostris* (in the eastern tropical Pacific) and *S. coeruleoalba* (in the western North Pacific). In a simple comparison of trends in reproductive parameters with population status (Table 11), the estimates do not behave entirely as would be predicted by the assumption of density-dependent response. For *S. longirostris*, age at attainment of sexual maturity is greater in the less exploited southern whitebelly population, as expected, and the ranking in pregnancy rate parallels status in the expected way, but length of lactation shows a trend the reverse of what would be expected, i.e. it is longest in the most-exploited population and shortest in the least-exploited population (due to the same trend in length of the 'resting period' Table 7). Perrin and Henderson (1984) found that estimated gross reproductive rate is not different (at $\alpha = 0.05$) in the eastern and northern whitebelly populations, although the former is probably at less than 25% of its original size and the latter at more than 75% of original (Smith, 1983).

For the heavily exploited population of *S. coeruleoalba* off Japan, Kasuya and Miyazaki (1975) estimated that pregnancy rate has increased and length of lactation decreased over the period 1952 to present but the lowest estimate of pregnancy rate and highest estimate of

Table 11

Comparison of trends in reproductive-parameter estimates to trends in status of populations in two delphinids. Rankings are of estimates from Tables 4, 6 and 7

	Percent of pre-exploitation size (rank: 1 is largest)	Age at attainment of sexual maturity (rank: 1 is highest)	Annual pregnancy rate (rank: 1 is lowest)	Length of lactation (rank: 1 is longest)
Stenella longirostris				
E. trop. Pacific				
S. whitebelly	1	—	1	3
N. whitebelly	2	1	2	2
Eastern	3	2	3	1
S. coeruleoalba				
W. Pacific				
1952–1958	1	—	2	2
1961–1968	2	—	1	1
1970–1973	3	—	3	3

length of lactation are for an intermediate period, 1961–68.

These simple comparisons suggest that reproductive parameters may behave in unexpected ways in a population under exploitation (see also section above on net reproductive rate).

Relationships Between Parameters

Ohsumi (1979) has extensively reviewed the topic of deductive modelling to estimate reproductive parameters. In the context of the present review, two cautionary points suggest themselves.

In any comparison across species or populations, care should be taken to use similarly derived estimates. For example, in modeling a relationship between size and other parameters (mortality rate, maximum net reproductive rate, etc.), the possible choices of measures of size include length at attainment of sexual maturity in males or females, average size of adult males or females, asymptotic length and other indices. Whatever the index used, it should be of the same parameter and calculated in the same way throughout. Further, and perhaps more difficult to ensure, any morphological or quantitative criteria used in estimating, e.g. the histological criteria of sexual maturity in males, should be comparable.

Another important point is that geographical variation should be taken into account in any analysis based on specimens that come from more than one location, or that come from only one population when considerable geographical variation is known to exist. Thus the results of an analysis relating mortality rate to body size across several species might be different (and probably more useful) if the component estimates included estimates for two or more populations of *Tursiops truncatus* than if they included only a pooled *Tursiops* estimate or an estimate for only one population. In a deductive analysis involving several parameters, it is, of course, essential that the estimates of input parameters for a species come from the same or similar populations of the species.

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[*Appendices 1–4 are on the following 8 pages*]

Appendix 1

Length data for delphinids. Sources listed for tabulated values; other sources consulted (which contributed to sample sizes) are included in Literature Cited

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal				Smallest mature animal				Largest individual				Source
					Male		Female		Male		Female		Male		Female		
	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	
Steno bredanensis																	Cadenat, 1949; Layne, 1965; Lütken, 1889; Perrin and E. Walker, 1975
All regions	87	(4)	—	—	—	—	—	—	216	(28)	212	(14)	265	(68)	255	(65)	
Sotalia fluviatilis																	Best and da Silva, 1984; Carvalho, 1963; Harrison and Brownell, 1971; van Utrecht, 1981
Coastal	59	(1)	92	(> 13)	157	(3)	170	(4)	167	(4)	162	(4)	187	(7)	182	(8)	
Riverine	71	(3)	83	(> 28)	138	(> 9)	132	(> 4)	140	(> 6)	139	(> 7)	152	(> 17)	149	(> 11)	
Sousa chinensis																	Blanford, 1888–91; Ross, 1979
All regions	—	—	97	(9)	—	—	—	—	—	—	—	—	320	(6)	244	(> 5)	
Sousa teuszii																	Cadenat and Paraiso, 1957; Cadenat, 1959
E. trop. Atlantic	—	—	—	—	—	—	—	—	—	—	—	—	248	(3)	235	(3)	
Peponocephala electra																	Bryden *et al.*, 1977; Perrin, 1976
All regions	65	(1)	112	(8)	212	(2)	229	(3)	264	(3)	257	(1)	273	(9)	257	(8)	
Feresa attenuata																	Best, 1970; Nishiwaki *et al.*, 1965; Perrin and Hubbs, 1969; Pryor *et al.*, 1965; Ross, 1979
All regions	53	(2)	82	(16)	—	—	—	—	216	(2)	221	(2)	264	(14)	243	(12)	
Pseudorca crassidens																	Mizue and Yoshida, 1961; Purves and Pilleri, 1978; Ross, 1979; Scott and Green, 1975; Tomilin, 1957
All regions	183	(> 10)	157	(> 429)	366	(12)	364	(> 10)	372	(28)	349	(> 54)	596	(> 119)	506	(> 253)	
Orcinus orca																	Allen, 1977; Anon. 1982b; Best and Ross, 1977; Carl, 1945; Christensen, 1982; Condy, van Aarde and Bester, 1978; Fiscus and Niggol, 1965; Ivashin, 1981; Jonsgård and Lyshoel, 1970; Mikhalev *et al.*, 1981; Nishiwaki and Handa, 1958; Pike and MacAskie, 1969; Ridgway, 1979; Scheffer, 1967; Tomilin 1957
All regions	274	(272)	183	(> 2,741)	617	(> 4)	488	(> 16)	520	(> 6)	457	(> 215)	975	(> 2,306)	853	(1,744)	
North Atlantic	255	(239)	183	(693)	559	(—)	488	(10)	660	(—)	457	(111)	975	(1,239)	853	(822)	
North Pacific	193	(1)	228	(134)	520	(2)	—	—	760	(1)	560	(1)	829	(> 56)	698	(52)	
South Pacific	140	(1)	200	(12)	—	—	—	—	—	—	—	—	805	(5)	670	(6)	
Indian Ocean	—	—	381	(37)	—	—	—	—	—	—	—	—	884	(25)	792	(12)	
Antarctic	250	(16)	320	(1,229)	—	—	370	(1)	—	—	540	(91)	910	(652)	762	(577)	
Globicephala melaena																	Anon., 1981a and 1982a; Budker, 1968; Duguy 1973–82; Duguy and Budker, 1972; Fraser, 1974; Gray, 1846; Guiler, 1978; Paulus, 1960; Sergeant, 1962
All regions	195	(308)	137	(3,629)	472	(65)	386	(> 471)	48	(> 5)	351	(89)	762	(> 1,398)	570	(2,086)	
E. North Atlantic	195	(2)	137	(206)	—	—	238	(> 5)	—	—	375	(5)	762	(88)	570	(56)	
W. North Atlantic	190	(306)	165	(3,399)	472	(65)	386	(466)	48	(> 5)	351	(84)	617	(> 1,378)	511	(2,020)	
New Zealand	—	—	177	(14)	—	—	—	—	—	—	—	—	600	(7)	500	(5)	
Tasmania	—	—	187	(95)	—	—	—	—	—	—	—	—	620	(40)	555	(55)	
G. macrorhynchus																	Alagarswami *et al.*, 1973; Hall *et al.*, 1971; Harrison *et al.*, 1972; Layne, 1965; Lowery, 1974; Perrin and Myrick, 1980; Ross, 1979; SEAN, 1977; van Bree *et al.*, 1978; Walker, 1975; Yonekura *et al.*, 1980
All regions	140	(25)	135	(661)	437	(16)	396	(17)	508	(3)	335	(6)	610	(> 231)	525–550	(> 344)	
W. North Atlantic	—	—	162	(369)	383	(1)	334	(3)	—	—	335	(2)	535	(> 95)	478	(> 146)	
E. North Pacific	104	(2)	135	(64)	352	(2)	336	(8)	—	—	396	(3)	590	(23)	480	(32)	
W. North Pacific	140	(17)	182	(153)	—	—	—	—	—	—	—	—	491	(51)	392	(102)	
Indian Ocean	—	—	168	(95)	437	(1)	396	(2)	508	(3)	405	(1)	610	(> 49)	525–550	(35)	

Lagenorhynchus obliquidens																	
North Pacific	102	(7)	124	(269)	198	(13)	216	(28)	170	(8)	170	(> 13)	230–234	(> 162)	236	(> 115)	Fiscus and Niggol, 1965; Harrison *et al.*, 1972; Harrison and McBrearty, 1977; Kasuya and Izumisawa, 1981; Scheffer and Slipp, 1948
L. acutus																	
North Atlantic	114	(> 59)	108	(233)	210	(16)	222	(6)	244	(4)	194	(51)	275	(> 99)	243	(> 83)	Sergeant *et al.*, 1980; Tomilin, 1957; van Utrecht, 1959
L. obscurus																	
Southern Hemisphere	—	—	92	(37)	—	—	130	(1)	—	—	170	(3)	211	(10)	193	(21)	Allen, 1977; Anon., 1978; Best, 1976; Brownell, 1974
L. cruciger																	
Southern Hemisphere	—	—	110	(3)	—	—		—	—	—	—	—	—	—	183	(2)	Brownell, in press; Fraser, 1966; Liouville, 1913; Nichols, 1908
L. albirostris																	
North Atlantic	125	(> 6)	119	(> 152)	257	(2)	249	(5)	251	(2)	250	(9)	315	(> 36)	305	(> 53)	Duguy, 1982; Fraser, 1974; Tomilin, 1957; van Utrecht, 1981; Weber, 1887
L. australis																	
E. South Pacific	—						—			—	—	—	216	(1)	—		Kellogg, 1941
Lagenodelphis hosei																	
All regions	45	(3)	95	(23)	184	(3)	231	(2)	264	(1)	226	(> 4)	264	(6)	264	(12)	Miyazaki and Wada, 1978; Perrin *et al.*,1973; Perrin and Leatherwood, in press; Ross, 1979;
Tursiops truncatus																	
All regions	122	(78)	84	(> 3,338)	314	(91)	295	(72)	202	(51)	190	(194)	381	(~ 1,400)	367	(~ 1,400)	Allen, 1977; Cadenat, 1959; Cornell, 1977; van Deinse, 1946; Duguy, 1974, 1976, 1980; Fraser, 1934, 1953; Gunter, 1942; Harmer, 1927; Harrison *et al.*, 1972; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Kasuya, 1973; Kasuya and Izumisawa, 1981, Kleinenberg, 1956; Leatherwood *et al.*, 1972; Norris and Prescott, 1961; Ross, 1977, 1979; SEAN, 1976, 1977, 1979; 1981; Sergeant *et al.*, 1973; Tomlin, 1957; True, 1889; Walker, 1981; Zeiller, 1977
E North Atlantic	91	(2)	116	(235)	314	(1)	295	(1)	—	—	312	(3)	381	(> 74)	350	(50)	
Mediterranean	—	—	140	(25)	160	(1)	—	—	—	—	300	(1)	330	(14)	320	(6)	
Black Sea	—	—	122	(> 1,450)	—	—	—	—	—	—	226	(> 4)	310	(~ 700)	234	(4)	
W North Atlantic[1]	117	(6)	92	(305)	210	(3)	—	—	—	—	232	(6)	310	(121)	339	(132)	
Florida coasts	112	(8)	95	(284)	277	(32)	238	(22)	242	(10)	225	(38)	290	(127)	276	(143)	
Gulf of Mexico[1]	122	(7)	91	(123)	—	—	239	(1)	218	(3)	229	(13)	380	(43)	367	(46)	
E. North Pacific (all forms)	—		110	(50)	269	(3)	264	(1)	263	(7)	276	(6)	340	(20)	330	(27)	
E. North Pacific (onshore)				—	269	(1)	255	(4)	297	(4)	—	—	333	(8)	307	(9)	
E. North Pacific (offshore)	—	—	114	(14)	234	(2)	264	(5)	263	(3)	276	(3)	310	(5)	290	(9)	
E tropical Pacific	88	(2)	—	—	236	(5)	242	(7)	244	(7)	243	(2)	266	(12)	256	(9)	
W North Pacific	120–129	(60)	—	—	292	(18)	280–289	(8)	288	(12)	250–259	(107)	335	(194)	320–329	(258)	
Indian Ocean (all forms)	60	(2)	84	(84)	278	(18)	280	(15)	202	(13)	190	(12)	327	(56)	280	(33)	
Indian Ocean ('*aduncus*')	60	(2)	84	(89)	235	(16)	220	(14)	202	(13)	190	(12)	254	(44)	252	(41)	
Indian Ocean ('*truncatus*')	—	—	270	(7)	278	(3)	280	(1)	—	—	—	—	327	(5)	280	(2)	
E. tropical Atlantic								—	—	—	—	—	368	(11)	350	(7)	
Grampus griseus																	
All regions	166	(10)	135	(> 243)	297	(15)	280–284	(14)	262	(10)	260–264	(22)	383	(> 81)	366	(69)	Duguy, 1974, 1979, 1981; Fraser, 1934, 1974; Kasuya and Izumisawa, 1981; Murie, 1870; Pillen and Gihr, 1969b; Ross, 1979; SEAN, 1976, 1980; Tomilin, 1957; True, 1889
Mediterranean	—	—	135	(62)	—	—	—	—	—	—	298	(1)	360	(11)	310	(10)	
E North Atlantic	166	(4)	173	(78)	244	(1)	—	—	—	—	320	(3)	383	(29)	366	(27)	
W North Atlantic	—	—	158	(25)	—	—	—	—	—	—	305	(5)	340	(9)	318	(12)	
W North Pacific	90–94	(4)	180–184	(43)	297	(11)	280–284	(10)	262	(9)	260–264	(13)	307	(20)	285–289	(23)	
S W Indian Ocean	84	(2)	163	(19)	243	(2)	257	(4)	—	—	291	(1)	325	(9)	277	(6)	
Stenella longirostris																	
All regions	84	(331)	70	(5,001)	192	(9,249)	190	(1,067)	160	(766)	152	(1,054)	235	(2,340)	204	(2,621)	Layne, 1965; Mead *et al.*, 1980; Oliver, Walker and Miller, 1982; Perrin, 1975a; Perrin *et al.*, 1977, 1979, 1981, Perrin and Henderson, 1984; Perrin and Oliver, 1982; Schmidly and Shane, 1978
Tropical Atlantic	81	(2)	90	(41)	158	(1)	190	(7)	173	(17)	177	(17)	208	(18)	204	(22)	
E tropical Pacific (Costa Rican)		—				—			181	(2)	193	(3)	216	(2)	203	(3)	
E tropical Pacific (eastern)	84	(169)	70	(2,566)	192	(594)	182	(608)	160	(356)	152	(536)	195	(1,102)	187	(1,297)	
E tropical Pacific (n. whitebelly)	82	(159)	72	(2,218)	191	(330)	188	(433)	160	(319)	157	(425)	203	(1,063)	195–199	(1,155)	
E. tropical Pacific (s. whitebelly)	—	—	85–89	(123)	—	—	—	—	167	(69)	162	(63)	235	(142)	190–194	(119)	

Appendix 1 (*continued*)

Species and region (stock in parentheses)	Largest fetus		Smallest individual		Largest immature animal				Smallest mature animal				Largest individual				Source
					Male		Female		Male		Female		Male		Female		
	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	cm	(*n*)	
S. clymene																	
Atlantic	—	—	—	—	—	—	188	(1)	184	(2)	—	—	196	(7)	188	(2)	Perrin *et al.*, 1981
S. plagiodon																	
Atlantic	—	—	120	(40)	—	—	—	—	—	—	—	—	223	(15)	226	(22)	Caldwell and Caldwell, 1966; SEAN, 1975, 1981
Stenella coeruleoalba																	
All regions	108	(114)	80	(6,236)	—	—	—	—	—	—	—	—	256	(> 2,272)	240–250	(> 2,239)	Duguy, 1980; Duguy *et al.*, 1978; Gurevich and Stewart, 1979; Kasuya, 1972; Miyazaki, 1977; Perrin and Oliver, 1982; Ross, 1979; SEAN, 1979
Mediterranean	—	—	80	(232)	—	—	—	—	—	—	—	—	220	(97)	215 220	(96)	
North Atlantic	—	—	116	(72)	—	—	—	—	—	—	194	(1)	248	(41)	244	(22)	
E. trop. Pacific	80	(13)	90	(202)	—	—	—	—	—	—	—	—	225–229	(103)	220	(99)	
W. North Pacific	108	(99)	95	(5,493)	240–250	(~ 127)	230–240	(~ 231)	200–210	(222)	200–210	(545)	256	(> 2,003)	240–250	(> 2,006)	
S.W. Indian Ocean	—	—	—	—	244	(5)	206	(1)	218	(5)	200	(5)	250	(16)	228	(10)	
S. attenuata																	
All regions	106	(562)	75–79	(6,347)	202	(> 259)	209	(440)	162	(> 820)	167	(> 1,462)	257	(> 3,566)	240–244	(> 3,235)	Allen, 1977; Best, 1969; Kasuya *et al.*, 1974; Nishiwaki *et al.*, 1965; Perrin, 1975a; Perrin *et al.*, 1976; Perrin and Oliver, 1982; Ross 1979
E. tropical Pacific (coastal)	—	—	90–94	(128)	—	—	—	—	203	(37)	184	(76)	257	(43)	240–244	(85)	
E. tropical Pacific (n. and s. offshore)	90	(468)	75–79	(5,348)	201	(> 150)	193	(307)	179	(> 724)	167	(> 1,127)	225–229	(> 3,141)	220–224	(> 2,792)	
Central Pacific	—	—	—	—	180	(1)	160	(1)	182	(6)	189	(3)	202	(8)	203	(4)	
W. North Pacific	—	—	89	(959)	202	(103)	209	(132)	162	(44)	173	(253)	234	(> 300)	220	(> 344)	
S.W. Indian Ocean	—	—	89	(9)	198	(3)	—	—	216	(2)	215	(1)	220	(5)	215	(5)	
Delphinus delphis																	
All regions	108	(> 446)	70	(> 45,650)	206	(33)	222	(> 1,973)	171	(> 5,090)	141–150	(> 8,583)	260	(> 27,211)	230	(> 26,368)	Allen, 1977; Aloncle, 1964; Anon., 1981a; Cadenat, 1957; 1959; Casinos and Vericad, 1976; Collet, 1981; Danilevskiy and Tyutyunnikov, 1968; Duguy, 1973, 1980; Evans, 1975; Fischer, 1881; Fraser, 1934, 1946, 1953, 1974; Guiler, 1978; Gurevich and Stewart, 1978; Hui, 1977; Kleinenberg, 1956; Legendre, 1926; Mercer, 1973; Mitchell, 1970; Ross, 1979; Scammon, 1874; SEAN, 1975; Sleptsov, 1941, Slijper, 1936; Tomilin, 1957; van Deinse, 1946, van Utrecht, 1981
Black Sea	95	(> 287)	70	(> 43,000)	171–180	(—)	161–170	(> 1,928)	171	(> 5,000)	141–150	(> 8,500)	219	(> 25,000)	196 200	(> 25,000)	
Mediterranean	—	—	120	(60)	—	—	—	—	—	—	—	—	222	(33)	208	(24)	
E. North Atlantic	108	(39)	84	(420)	206	(12)	194	(14)	206	(16)	174	(18)	258	(126)	230	(272)	
W. North Atlantic	—	—	—	—	—	—	—	—	—	—	212	(1)	236	(8)	212	(15)	
E. N. Pacific (Baja neritic)	—	—	—	—	—	—	—	—	—	—	—	—	240–244	(~ 16)	206	(2)	
E. N. Pacific (n. temp. offshore)	80–84	(40)	80–84	(> 109)	—	—	—	—	—	—	—	—	179	(5)	195	(8)	
E. tropical Pacific (n. trop.)[2]	> 80–89	(25)	75–79	(453)	—	—	—	—	—	—	—	—	240–244	(216)	220–224	(236)	
E. tropical Pacific (cent. trop.)	80–89	(81)	65–69	(1,468)	—	—	—	—	176–180	(40)	176 180	(48)	235–239	(741)	205 210	(625)	
W. South Pacific	84	(1)	91	(31)	199	(5)	174	(5)	203	(5)	198	(3)	260	(> 19)	209	(16)	
W. North Pacific	—	—	128	(22)	—	—	—	—	—	—	—	—	197	(7)	187	(13)	
S.W. Indian Ocean	85	(3)	90	(26)	186	(6)	222	(8)	236	(4)	212	(1)	254	(13)	222	(12)	
E. tropical Atlantic	76	(7)	123	(72)	—	—	197	(1)	189	(9)	198	(5)	235	(34)	222	(31)	
Lissodelphis borealis																	
North Pacific	—	—	114	(49)	212	(4)	200	(2)	220	(7)	201	(9)	307	(23)	229	(22)	Leatherwood and Walker, 1979; Sullivan and Houck, 1979
L. peronii																	
S. Hemisphere	—	—	184	(10)	—	—	—	—	—	—	—	—	~ 210	(5)	~ 230	(5)	Baker, 1981; True, 1889
Cephalorhynchus hectori																	
New Zealand	48	(1)	85	(18)	—	—	—	—	—	—	153	(1)	137	(10)	153	(4)	Abel *et al.*, 1971; Anon., 1981a and 1982a; Baker, 1978; Mörzer-Bruyns and Baker, 1973
C. eutropia																	
No data	—					—	—	—		—			—			—	
C. heavisidii																	
No data	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	
C. commersonii																	
W. South Atlantic	—	—	92	(37)	—	—	144	(2)	136	(1)	—	—	137	(15)	146	(10)	Harmer, 1922; Lockyer *et al.*, 1981; Spotte *et al.*, 1979

[1] Exclusive of Florida.

[2] May include some 'Baja neritic' (on the average larger).

Appendix 2

Testis data for delphinids

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(*n*)	g	(*n*)	
Steno bredanensis					
W. North Pacific	175	(9)	1,150	(9)	Miyazaki, 1980
Sotalia fluviatilis					
Amazon basin	27	(7)	1,060	(10)	Best and da Silva, 1984; Harrison and Brownell, 1971
Peponocephala electra					
W. trop. Pacific	674	(3)	685	(3)	Bryden *et al.*, 1977
Central trop. Atlantic	~ 1,100[1]	(1)	~ 1,100[1]	(1)	Goodwin, 1945
Feresa attenuata					
Central trop. Pacific	321	(1)	377	(1)	Pryor *et al.*, 1965
Pseudorca crassidens					
W. North Pacific	~ 1,700[1]	(21)	~ 7,400[1]	(31)	Kasuya and Izumisawa, 1981
Orcinus orca					
All regions	—	—	23,100	(64)	Ross, 1979; Allen, 1977; Mikhalev *et al.*, 1981; Harrison *et al.*, 1972
Antarctic	—	—	23,100	(57)	Mikhalev *et al.*, 1981
Globicephala melaena					
E. North Atlantic	575	(12)	7,200	110)	Sergeant, 1962
G. macrorhynchus					
S.W. Indian Ocean	770	(4)	3,540	(4)	Ross, 1979
E. trop. Pacific	264[2]	(7)	548[2]	(10)	Walker, 1981
W. North Pacific	~ 50[1]	(12)	~ 700[1]	(29)	Kasuya and Izumisawa, 1981
W. South Pacific	505	(1)	572	(8)	Ross, 1979
S.W. Indian Ocean ('*aduncus*')	318	(5)	800	(5)	Ross, 1979
Grampus griseus					
E. North Pacific	3,130	(3)	6,360	(3)	Orr, 1966; Harrison *et al.*, 1972
W. North Pacific	~ 350[1]	(9)	~ 5,300[1]	(20)	Kasuya and Izumisawa, 1981
Lagenorhynchus obliquidens					
E. North Pacific	548	(16)	559	(16)	Harrison *et al.*, 1972
W. North Pacific	~ 170[1]	(25)	~ 390[1]	(87)	Kasuya and Izumisawa, 1981
L. obscurus					
E. South Atlantic	—	—	800	(—)	Best, 1976
L. acutus					
W. North Atlantic	180	(5)	370	(21)	Sergeant *et al.*, 1980
Lagenodelphis hosei					
W. North Pacific	990	(1)	990	(1)	Tobayama *et al.*, 1973
S.W. Indian Ocean	1,280	(1)	1,280	(2)	Ross, 1979
Tursiops truncatus					
All regions	~ 50[1]	(45)	983	(98)	Below, and Harrison and Fanning, 1974, Allen, 1977 and Leatherwood, 1978

[1] Estimated as ½ combined testis weight.

[2] Includes epididymis.

Appendix 2 (*continued*)

Species and region (stock in parentheses)	Minimum weight of 'adult' testis		Maximum weight of testis		Source
	g	(*n*)	g	(*n*)	
Florida and Gulf of Mexico	280	(6)	532	(19)	Harrison *et al.*, 1972; Sergeant *et al.*, 1973; Harrison and Ridgway, 1971;
E. North Pacific (onshore)	536	(4)	983	(5)	Walker, 1981
E. North Pacific (offshore)	248	(3)	530	(5)	Walker, 1981
S. attenuata					
E. trop. Pacific (offshore)	100[2]	(> 207)	~ 1,200[1, 2]	(> 415)	Harrison, 1969; Harrison *et al.*, 1972; Perrin *et al.*, 1976
W.N. Pacific	66	(142)	~ 650[1]	(> 138)	Kasuya *et al.*, 1974; Kasuya, 1976
S.W. Indian Ocean	—	—	121	(5)	Ross, 1979
Stenella longirostris					
Gulf of Mexico	320	(9)	980	(12)	Mead *et al.*, 1980; Layne, 1965
E. trop. Pacific (eastern)	20–30[2]	(50)	800–900	(826)	Perrin *et al.*, 1977; Perrin and Henderson, 1984
E. trop. Pacific (n. whitebelly)	60–80[2]	(92)	1,354[2]	(695)	Perrin and Henderson, 1984
Centr. trop. Pacific	—	—	330	(8)	Harrison *et al.*, 1972; Allen, 1977;
E. trop. Atlantic	—	—	925	(2)	Cadenat and Doutre, 1959
S. coeruleoalba					
E. trop. Pacific	—	—	~ 157[1, 2]	(38)	Gurevich and Stewart, 1979
W. North Pacific	8	(> 222)	~ 250[1]	(> 437)	Kasuya, 1976; Miyazaki, 1977; Hirose and Nishiwaki, 1971
S.W. Indian Ocean	94	(2)	136	(2)	Ross, 1979
Delphinus delphis					
Black Sea	300	(—)	1,000	(2,138)	Sleptsov, 1941
E. North Atlantic	100	(9)	800	(20)	Collet and St. Girons, 1984
E. North Pacific (offshore)	465	(12)	1,672	(31)	Harrison, 1969; Harrison *et al.*, 1972; Ridgway and Green, 1967
E. trop. Pacific (centr. trop.)	129	(12)	853	(42)	Oliver, 1973
S.W. Indian Ocean	1,815	(3)	4,085	(3)	Ross, 1979
E. trop. Atlantic	—	—	883	(7)	Cadenat, 1959
Lissodelphis borealis					
E. North Pacific	705	(2)	705	(3)	Harrison *et al.*, 1972; Sullivan and Houck, 1979
Cephalorhynchus hectori					
W. South Pacific	—	—	465	(1)	Baker, 1978

[1] Estimated as ½ combined testis weight.

[2] Includes epididymis.

Average length of adults and asymptotic length in delphinids. Minimum sample size for inclusion is at least 2 for at least one column. Standard deviation given for sample size of 25 or more, where possible

Species and region (stock in parentheses)	Average length of sexually mature animals						Asymptotic length				Source
	Males			Females			Males		Females		
	cm	(*n*)	SD	cm	(*n*)	SD	cm	(*n*)	cm	(*n*)	
Steno bredanensis											
W. North Pacific	232	(24)	—	231	(11)	—	—	—	—	—	Miyazaki, 1980
E. trop. Atlantic	227	(3)	—	234	(1)	—	—	—	—	—	Cadenat, 1959
Sotalia fluviatilis											
Coastal	177	(4)	—	176	(4)	—	—	—	—	—	van Utrecht, 1981
Riverine	146	(6)	—	145	(7)	—	—	—	—	—	Best and da Silva, 1984; Carvalho, 1963
Sousa teuszii											
E. trop. Atlantic	200	(3)	—	—	—	—	—	—	—	—	Allen, 1977
Peponocephala electra											
E. South Pacific	268	(3)	—	—	—	—	—	—	—	—	Bryden *et al.*, 1977
Pseudorca crassidens											
E. North Atlantic	532	(4)	—	447	(14)	—	541	(3)	452	(10)	Peacock *et al.*, 1936; Purves and Pilleri, 1978
W. North Atlantic	520	(1)	—	458	(2)	—	—	—	—	—	Odell *et al.*, 1980
W. North Pacific	—	—	—	430	(92)	27.1	—	—	—	—	Kasuya and Izumisawa, 1981; Mizue and Yoshida, 1961
W. South Pacific	—	—	—	400	(18)	—	—	—	—	—	Scott and Green, 1975
Orcinus orca											
E. North Atlantic	945	(1)	—	566	(110)	65.5	—	—	—	—	Christensen, 1982; Gray, 1846; Jonsgård and Lyshoel, 1970
Antarctic	—	—	—	645	(91)	56.6	—	—	—	—	Mikhalev *et al.*, 1981
Globicephala melaena											
W. North Atlantic	545	(12)	—	381	(85)	11.5	~ 550	(> 4)	~ 460	(> 19)	Sergeant, 1962
G. macrorhynchus											
W. North Atlantic	—	—	—	345	(2)	—	~ 470	(—)	~ 360	(—)	Harrison *et al.*, 1972; Irvine *et al.*, 1979
E. North Pacific	—	—	—	466	(2)	—	—	—	—	—	Harrison *et al.*, 1972
W. North Pacific	453	(13)	—	358	(72)	14.2	—	—	330–360	—	Yonekura *et al.*, 1980
Lagenorhynchus obliquidens											
E. North Pacific	190	(8)	—	192	(12)	—	—	—	—	—	Fitch and Brownell, 1968; Harrison *et al.*, 1972; Ridgway and Green, 1967
L. acutus											
W. North Atlantic	250	(4)	—	224	(30)	6.0	—	—	—	—	Sergeant *et al.*, 1980
L. obscurus											
E. South Atlantic	188	(2)	—	191	(1)	—	—	—	—	—	Best, 1976
L. albirostris											
E. North Atlantic	260	(2)	—	259	(9)	—	—	—	—	—	Duguy, 1982; van Bree and Husson, 1964; van Utrecht, 1981
Lagenodelphis hosei											
All regions (4)	236	(3)	—	235	(7)	—	234	(7)	241	(4)	Perrin *et al.*, 1973; Ross, 1979; SEAN, 1978; Tobayama *et al.*, 1973
Tursiops truncatus											
Black Sea	275	(—)	—	233	(—)	—	—	—	—	—	Kleinenberg, 1956
W. North Atlantic¹	—	—	—	252	(6)	—	—	—	—	—	Leatherwood *et al.*, 1972
Florida (both coasts)	258	(13)	—	239	(45)	8.7	270	(7)	250	(13)	Cornell, 1977; Harrison *et al.*, 1972; Harrison and McBrearty, 1977; Sergeant *et al.*, 1973; Zeiller, 1977
Gulf of Mexico¹	241	(4)	—	251	(12)	—	—	—	259	(1)	Gunter, 1942; Harrison *et al.*, 1972; Harrison and McBrearty, 1977, Schmidly, 1978
E. N. Pacific (onshore)	—	—	—	312	(4)	—	—	—	—	—	Walker, 1981
E. N. Pacific (offshore)	283	(3)	—	282	(3)	—	—	—	—	—	Walker, 1981
E. trop. Pacific	256	(7)	—	250	(2)	—	—	—	—	—	Walker, 1981
W. North Pacific	—	—	—	288	(138)	13.4	—	—	—	—	Kasuya and Izumisawa, 1981
Indian Ocean ('*aduncus*')	239	(15)	—	237	(26)	—	239	(5)	241	(14)	Allen, 1977; Harrison and Fanning, 1973; Harrison and McBrearty, 1977; Ross, 1979

Appendix 3 (*continued*)

Species and region (stock in parentheses)	Average length of sexually mature animals: Males cm	Males (*n*)	Males SD	Females cm	Females (*n*)	Females SD	Asymptotic length: Males cm	Males (*n*)	Females cm	Females (*n*)	Source
Grampus griseus											
E. North Atlantic	—	—	—	332	(5)	—	370	(1)	342	(1)	Flower, 1872; Fraser, 1934, 1946; Harmer, 1927; Murie, 1870; Tomilin, 1957
W. North Pacific	288	(9)	—	276	(13)	—	—	—	—	—	Kasuya and Izumisawa, 1981
Stenella longirostris											
Gulf of Mexico	192	(15)	—	189	(17)	—	201	(1)	201	(1)	Mead *et al.*, 1980; Layne, 1965
E. trop. Pacific (Costa Rican)	192	(2)	—	—	—	—	—	—	—	—	Perrin, 1975a
E. trop. Pacific (eastern)	176	(594)	6.0	171	(560)	6.1	180	(12)	171	(60)	Perrin *et al.*, 1977, 1979; Perrin and Oliver, 1982
E. trop. Pacific (n. whitebelly)	179	(319)	7.0	176	(425)	6.8	180	(21)	175	(28)	Perrin and Henderson, 1984
E. trop. Pacific (s. whitebelly)	181	(69)	6.6	178	(63)	7.3	—	—	—	—	Perrin *et al.*, 1979; Perrin and Oliver, 1982
S. clymene											
Atlantic	185	(3)	—	—	—	—	—	—	—	—	Perrin *et al.*, 1981
S. coeruleoalba											
E. trop. Pacific	—	—	—	—	—	—	205	(3)	200	(2)	Gurevich and Stewart, 1979
W. North Pacific	227	(157)	—	220	(151)	—	238	(214)²	225	(584)²	Miyazaki, 1977
S.W. Indian Ocean	235	(5)	—	218	(5)	—	244	(1)	217	(2)	Ross, 1979
S. attenuata											
E. trop. Pacific (coastal)	228	(32)	10.7	209	(70)	9.0	—	—	—	—	Perrin, 1975a; Perrin and Oliver, 1982
E. trop. Pacific (n. and s. offshore)	201	(730)	8.5	187	(1,123)	7.0	200	(—)	190	(—)	Harrison *et al.*, 1972; Perrin *et al.*, 1979; Perrin and Oliver, 1982
W. North Pacific	204–207	(80)	—	192–195	(251)	—	207	(—)	194	(135)²	Harrison *et al.*, 1972; Kasuya, 1976; Kasuya *et al.*, 1974; Nishiwaki *et al.*, 1974
S.W. Indian Ocean	217	(3)	—	215	(2)	—	—	—	215	(1)	Best, 1969; Ross, 1979
Delphinus delphis											
Black Sea	178	(890)	—	(a) 170 (b) 175	(1,809) (25)	— 9.4	—	—	—	—	Mal'm and Trotskaya, 1932; Mayarova and Danilevskiy, 1934; Slepstov, 1941; Sokolov, 1962
E. North Atlantic	219	(17)	—	193	(23)	—	243	(1)	211	(3)	Collet, 1981; Fischer, 1881, Fraser, 1934; Slijper, 1936; van Utrecht and Husson, 1968
W. North Atlantic	—	—	—	211	(2)	—	—	—	—	—	Mercer, 1973; Ulmer, 1981
E. trop. Pacific (centr. trop.)	208	(40)	—	196	(48)	—	—	—	—	—	Evans, 1975
W. South Pacific	219	(5)	—	201	(3)	—	—	—	—	—	Allen, 1977; van Utrecht, 1981
S.W. Indian Ocean	242	(4)	—	212	(1)	—	—	—	212	(1)	Ross, 1979
E. trop. Atlantic	210	(9)	—	208	(5)	—	—	—	—	—	Cadenat, 1959
Lissodelphis borealis											
E. North Pacific	263	(7)	—	217	(9)	—	—	—	—	—	Leatherwood and Walker, 1979; SEAN, 1981; Sullivan and Houck, 1979
Cephalorhynchus commersonii											
W. South Atlantic	136	(1)	—	—	—	—	130	(6)	139	(2)	Lockyer *et al.*, 1981; Spotte *et al.*, 1979

[1] Exclusive of Florida.
[2] Total in analysis, mature and immature.

Appendix 4

Average age and maximum age of sexually mature delphinids, in years (y) or GLGs – terminology of Perrin and Myrick 1980 – (G)

Species and region (stock in parentheses)	Average age of sexually mature				Maximum age of sexually mature				Source
	Males		Females		Males		Females		
	y or G	(*n*)	y or G	(*n*)	y or G	(*n*)	y or G	(*n*)	
Steno bredanensis									
W. North Pacific	20y	(24)	21y	(10)	32y	(24)	30y	(11)	Miyazaki, 1980
Peponocephala electra									
W. South Pacific	27G	(2)	12G	(1)	47G	(2)	12G	(1)	Bryden *et al.*, 1977
Feresa attenuata									
S.W. Indian Ocean	14G	(2)	—	—	14G	(2)	—	—	Ross, 1979
Pseudorca crassidens									
E. North Atlantic	16y	(3)	17y	(3)	20y	(33)	22y	(40)	Purves and Pilleri, 1978
Orcinus orca									
All regions	—	—	—	—	35G	(56)	34G	(68)	Christensen, 1980; Mitchell, 1980; Ross, 1979
Globicephala melaena									
W. North Atlantic	> 11y	(58)	> 13y	(203)	26G, 14y	(165)	> 19G, > 20y	(296)	Perrin and Myrick, 1980; Ross, 1970; Sergeant, 1962
G. macrorhynchus									
W. North Atlantic	—	—	—	—	21G	(6)	49G	(11)	Perrin and Myrick, 1980; Ross, 1979
W. North Pacific	—	—	—	—	30G	(7)	> 29G	(3)	
S.W. Indian Ocean	13G	(2)	14G	(1)	15G	(2)	14G	(1)	
Lagenorhynchus obscurus									
E. South Atlantic	—	—	—	—	7y	(1)	21y	(2)	Best, 1976
L. acutus									
W. North Atlantic	—	—	12G	(26)	22G	(14)	27G	(38)	Sergeant *et al.*, 1980
Tursiops truncatus									
All regions	19y, > 12G	(17)	> 26y, > 11G	(26)	25y, 25G	(158)	> 30y, 27G	(166)	Hohn, 1980; Ross, 1977, 1979; Sergeant *et al.*, 1973
W. North Atlantic	19y	(6)	> 19y	(17)	25y, 25G	(90)	> 30y, 27G	(98)	
S.W. Indian Ocean	> 12G	(11)	> 11G	(6)	> 17G	(11)	13G	(6)	
('*aduncus*')									
Grampus griseus									
S.W. Indian Ocean	—	—	> 13G	(2)	> 13G	(2)	> 17G	(2)	Ross, 1979
Stenella longirostris									
Gulf of Mexico	9G	(2)	12G	(2)	10G	(3)	12G	(4)	Mead *et al.*, 1980; Perrin *et al.*, 1977; Perrin and Henderson, 1984
E. trop. Pacific (eastern)	7–10y	(39)	—	—	12–15y	(182)	15–21y	(250)	
E. trop. Pacific (n. whitebelly)	8–12y	(57)	—	—	13–19y	(170)	16–23y	(270)	
S. coeruleoalba									
E. trop. Pacific	—	—	—	—	16G	(38)	15G	(48)	Gurevich and Stewart, 1979; Miyazaki, 1977
W. North Pacific	14y	(222)	14y	(541)	29y	(222)	28y	(541)	
S attenuata									
E. trop. Pacific (n. offshore)	> 11G	(42)	—	—	> 17G	(42)	> 17G	(209)	Kasuya, 1976; Perrin *et al.*, 1976
W. North Atlantic	—	—	—	—	40y	(158)	46y	(200)	
Delphinus delphis									
Black Sea	—	—	15y	(17)	22y	(—)	20y	(17)	Kleinenberg and Klevezal', 1962
E. North Atlantic	—	—	—	—	> 12G	(5)	> 9G	(4)	Collet and St. Girons, 1984
Cephalorhynchus commersonii									
W. South Atlantic	—	—	—	—	15G	(13)	11G	(7)	Lockyer *et al.*, 1981

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Reproductive Estimates as a Source of Information on Survival Rates

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ABSTRACT

A method of estimating the survival rates and net rates of population increase is based on estimates of the proportion of animals which are mature, the average age at attainment of sexual maturity, and the adult fecundity rate. The method is most useful for exploring the ranges of survival rates that are consistent with the estimates of these parameters. Several assumptions are necessary to obtain survival-rate estimates, including constancy of survival and fecundity rates and a stable age distribution. The method is applied to data from three dolphin populations in the eastern tropical Pacific. These data are not consistent with a positive net rate of population increase, but several possible sampling biases exist for the data and must be investigated.

INTRODUCTION

Estimates of survival rates for natural animal populations and especially for marine mammals are difficult to obtain. Analysis of the age structure of a population is perhaps the easiest and most often used approach for obtaining survival estimates (Seber, 1973). However, it may be impossible or impractical to determine the age of a sample of individuals from a population. In contrast, it is often relatively straightforward to classify individuals according to their reproductive state. In many organisms, certain of the reproductive states are of relatively constant duration and may provide a classification of individuals into separate age groupings. Such age groupings have the potential to provide information on survival rates.

In this paper, a method is developed for estimating survival rates using the classification of animals into mature and immature classes. This method is applied to available reproductive data for dolphin populations in the eastern tropical Pacific. The method is not meant to produce precise estimates of survival but is meant to explore the range of survival rates that can be considered both biologically reasonable and consistent with the data.

METHODS

The method requires prior estimates of three parameters and is based on four specific assumptions. The three parameters are:

1. the proportion of females which are mature,
2. the average adult female fecundity rate, and
3. the age at attainment of sexual maturity.

The first two parameters should be directly estimable from random samples collected for reproductive information. While estimating the age of maturation requires some aging information, it may often be a much easier quantity to estimate than the entire age structure of the population and may even be available from independent sources such as from tagged or captive animals.

The problem then becomes one of finding the sets of survival rates that are consistent with the observed values for these reproductive parameters. To answer this problem, some assumptions about the age structure and age-specific vital rates are needed, namely:

1. the survival rate from birth to the age at attainment of maturity is constant,
2. the survival rate past the age at attainment of maturity is constant (but not necessarily equal to the juvenile rate),
3. the fecundity rate (i.e. the number of females born to a mature female) of mature animals is constant, and
4. the population is in a stable age distribution.

The fourth assumption, that of a stable age distribution, underlies any method of estimating survival rates from the age structure of a population (Seber, 1973). Some alternatives to the other three assumptions are discussed below.

The model used in this paper is based on a Leslie projection matrix modified to include a survival value in the lower right-hand corner:

$$\vec{\mathbf{N}}(t+1) = \tilde{M}\vec{\mathbf{N}}(t) \qquad (1)$$

where

$$\tilde{M} = \begin{matrix} 0 & 0 & \cdots & \cdots & 0 & F_A \\ S_1 & 0 & & & 0 & 0 \\ 0 & S_2 & & & \cdot & \cdot \\ \cdot & 0 & \cdot & & & \cdot \\ \cdot & \cdot & & \cdot & & \\ \cdot & & & & 0 & 0 \\ 0 & \cdots & \cdots & 0 & S_m & S_A \end{matrix}$$

and where

$\vec{\mathbf{N}}(t)$ = a vector of the number of females in each age class 1 to m, and the $m+1$ element equals the number of females older than age m (i.e. the number of mature females),
m = the age at attainment of maturity,
S_A = the adult survival rate,
$S_i = S_j$ = a constant for $i = 1$ to m (i.e. the juvenile survival rate), and
F_A = the adult female fecundity rate.

The use of S_A in the lower right hand corner of the matrix $\tilde{M}$ collapses the size of the projection matrix when survival rates past a certain age are assumed constant. It is well known that a population growing according to a matrix of this form will approach a stable age distribution corresponding to the dominant eigenvector of the matrix. Thus, given the input parameters and the above matrix, any combinations of juvenile survival (S_j) and adult survival (S_A) rates that would yield a stable age distribution in which the proportion mature equals the observed proportion mature could be considered reasonable estimates of the survival rates. The problem of solving for values of S_j and S_A can be reduced to the following two equations (see Appendix):

$$1 = (S_j/\lambda)^m + (F_A/\lambda) + S_A/\lambda \qquad (2)$$

$$R = \frac{(S_j/\lambda)^m F_A + S_A}{F_A \sum_{i=1}^{m+1} (S_j/\lambda)^{i-1} + S_A} \qquad (3)$$

with symbols defined as above, and where

$\lambda =$ the largest eigenvalue of the matrix $\tilde{M}$, or the net rate of increase of the population, and

$R =$ the proportion of females which are mature.

Equations 2 and 3 represent two equations in three unknowns (S_j, S_A, and λ). If the value of any one of the three unknowns is specified, the other two are uniquely determined. If the assumption is made that the age distribution is stationary (i.e. $\lambda = 1$, Seber, 1973), then the method provides a specific set of survival estimates for a set of input parameters. This assumption usually underlies most survival-rate estimates made from age-structured data (Seber, 1973). However, if the net rate of increase is unknown and there are reasons to suspect that the population's age structure may not be stationary, it may be more informative to examine the combinations of survival rates and net rates of increase consistent with the input parameters. For the examples of dolphin populations considered in this paper, there are reasons to suspect that the population's age structure may not be stationary (Smith, 1983). Thus, solutions for the juvenile survival rate and the net rate of increase will be presented as a function of adult survival rate in order to explore biologically meaningful sets of estimates.

To illustrate this method, survival estimates are presented based on estimates of the reproductive parameters for the northern-offshore-spotted population of *Stenella attenuata* and the eastern-spinner and northern-whitebelly-spinner populations of *Stenella longirostris*. One-half the estimated pregnancy rate is used as an estimate of fecundity. The estimated proportion of mature females and the pregnancy rates are based on the pooled data base for 1973 to 1978 for each of the three stocks. (Method 1 of Henderson, Perrin and Miller, 1980). Method 2 of Henderson *et al.* has been shown to be invalid (Perrin and Reilly, 1984). The estimated ages at attainment of maturity are based on the ages estimated in Perrin, Coe and Zweifel (1976), Perrin, Holts and Miller (1977) and Perrin and Henderson (1984). The parameters used are shown in Table 1.

In considering the results, two criteria were used to determine the range of estimated survival rates consistent with the data and biological reality. The first criterion is the biological constraint that survival rates must be less than or equal to one. The second criterion is that juvenile rates must be less than or equal to adult survival rates. While this criterion is not absolute, it is usually considered a characteristic of the survival curve for long-lived organisms (Caughley, 1966).

Table 1

Parameters values used for estimating survival rates for the three dolphin stocks

	Northern offshore spotted	Eastern spinner	Northern whitebelly spinner
Age at attainment of maturity	8[1]	5[2]	6[2]
Proportion mature[3]	0.561	0.432	0.522
Pregnancy rate[3]	0.376	0.339	0.356

[1] Rounded to the nearest year from the estimate in Perrin *et al.*, 1976.

[2] Rounded to the nearest year from the estimate in Perrin and Henderson, 1984.

[3] From Henderson *et al.*, 1980.

RESULTS

Fig. 1 provides an example of estimates S_j and λ plotted as a function of adult survival rates for the northern-whitebelly-spinner population. The dotted lines corresponding to $S_j = S_A$ and $S_j = 1$ represent the upper bound for the survival rates corresponding to the two criteria listed in the methods section. Thus, for example, the highest estimates of juvenile and adult survival meeting both criteria in this figure is 0.81, which corresponds to a net rate of increase of 0.89. Similarly, biological limits are reached when $S_j = 1.00$ in this figure, with corresponding values of $S_A = 0.91$ and $\lambda = 1.05$. Also indicated in this figure is the line where $\lambda = 1.00$

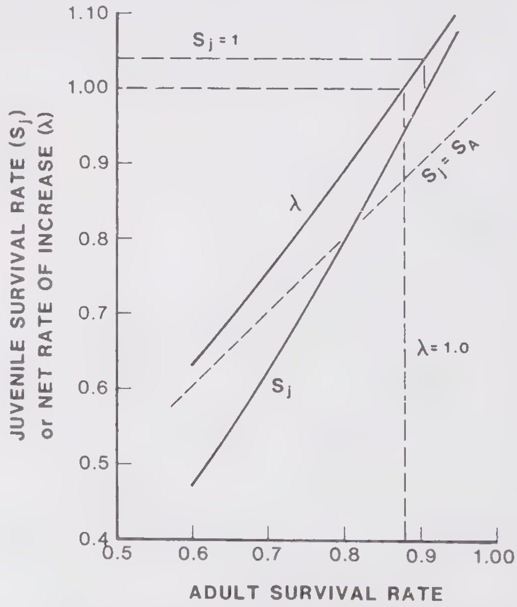

Fig. 1. Estimates of juvenile survival rate (S_j) and net rate of increase (λ) plotted as a function of adult survival rate (S_A) for the northern-whitebelly-spinner population of *Stenella longirostris*.

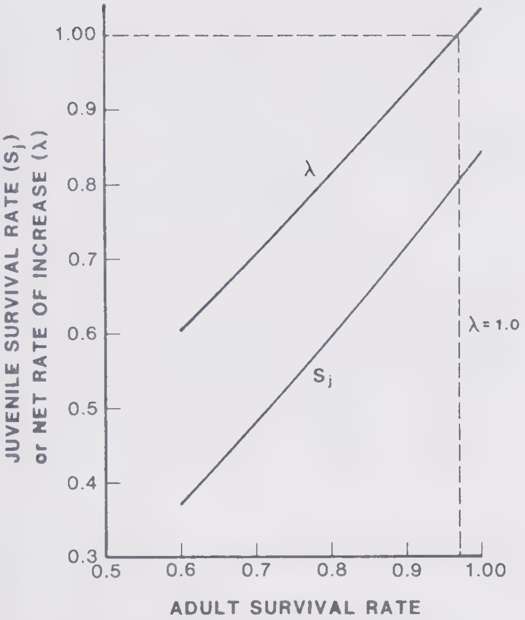

Fig. 2. Estimates of juvenile survival rate (S_j) and net rate of increase (λ) plotted as a function of adult survival rate (S_A) for the northern-offshore-spotted population of *Stenella attenuata*.

Table 2

Estimates of juvenile survival rate (S_j) and the net rate of increase (λ) as a function of adult survival rate (S_A) for the northern offshore spotted dolphin (*Stenella attenuata*) based on the parameter values in Table 1

S_A	S_j	λ
0.60	0.368	0.603
0.70	0.478	0.708
0.80	0.594	0.815
0.90	0.715	0.924
0.95	0.777	0.980

($S_A = 0.88$ and $S_j = 0.94$), since, from a management perspective, this may be a critical point. In Fig. 2, the results for the northern-offshore-spotted population have been plotted to illustrate a different constraint on the estimates. In this case, the estimates are constrained by biological limits on adult survival rates, with a corresponding maximum possible value for S_j being 0.84 and for $\lambda = 1.03$.

Results for all three populations are presented in Tables 2–4. Note, as is the case for the eastern-spinner population (Table 3), that real-valued solutions may not exist for Equations 2 and 3, since the proportion mature (R) considered as a function of S_j for a fixed value of S_A has a minimum which can be above the observed value under consideration. While the results in this table suggest that a wide range of adult and juvenile survival rates are consistent with the observed data (except for the eastern-spinner population), none of the tabled values yield non-negative growth rates if the two criteria given in the methods section are applied. Estimated growth rates equal to or greater than one are not possible for the survival rates less than one for the observed data from the eastern-spinner population. For the northern-whitebelly-spinner population, growth rates greater than one are not possible unless juvenile survival rates exceed adult survival rates. For the northern-offshore-spotted population, net growth rates greater than one require that the survival rate for adults be extremely high (~ 0.97), especially considering that the model makes no provision for senescence. Thus, in a population in which adult survival is constant and equal to 0.97 and the age at attainment of maturity is 8, approximately 28% of the adult population would be over age 50.

Table 3

Estimates of the juvenile survival rate (S_j) and the net rate of increase (λ) as a function of adult survival rate (S_A) for the eastern spinner dolphin (*Stenella longirostris*) based on parameter values in Table 1

S_A	S_j	λ
0.40	0.399	0.473
0.50	0.771	0.727
0.60	*	*
0.70	*	*
0.80	*	*
0.90	*	*
0.95	*	*

* No solution for the juvenile survival rate exists that will balance this version of the matrix for the combination of values for adult survival rates, fecundity rate and age of maturity.

Table 4

Estimates of juvenile survival rate (S_j) and the net rate of increase (λ) as a function of adult survival rate (S_A) for the northern whitebelly spinner dolphin (*Stenella longirostris*) based on the parameter values in Table 1

S_A	S_j	λ
0.60	0.469	0.630
0.70	0.620	0.755
0.80	0.790	0.888
0.90	0.980	1.031
0.95	1.083	1.107

DISCUSSION

The method presented in this paper provides a way to estimate survival rates from minimal data. Although a number of restrictive assumptions about the shape of the age-specific survival and fecundity curves are made, there are a number of ways that the matrix $\tilde{M}$ in equation 1 could be re-parameterized and still be solvable. Such re-parameterizations can be used to explore the sensitivity of a set of estimates to these assumptions. For example, for long-lived mammals, survival rates are usually considered to be increasing from birth to the age at attainment of maturity. To explore the effect of this type of survival curve, the constant juvenile survival rate in the matrix $\tilde{M}$ could be replaced by an increasing function, so that the survival rate at any age between birth and the age of maturity was a function of the estimated survival rate at birth and an animal's present age. In the limit, the effect of this assumption can be examined by assuming that the only difference in juvenile and adult survival rates occurs during the first year of life. In a similar manner, the effects of assuming constant adult survival and fecundity rates can be explored, as long as the matrix contains only two unknown parameters. Thus, by considering a number of parameterizations for the projection matrix, it would be possible to refine the range of survival rates which are consistent with an observed set of data. In Polacheck (1983), a number of these different parameterizations of the projection matrix for the dolphin example were considered, and the basic results were insensitive to the different matrices.

The effect of the assumption of a stable age distribution is harder to assess. However, the method depends on the assumption of a stable age distribution only in order to compare the observed proportion mature with the proportion mature in a stable age distribution. Since the observed proportion mature is obtained as an average across a number of age classes, this method should be less sensitive to stochastic variations around a stable age distribution and sampling errors than are methods which use the entire age distribution.

The results of the application of this method to the example presented in this paper are rather disturbing, as they suggest that the only estimates of survival rates consistent with the data and with a non-declining net rate of increase are either biologically impossible or unreasonable. The difficulty in obtaining both biologically reasonable estimates of survival rate and estimates of a net rate of growth greater than one are not the same for all three populations. The spinner populations are constrained by biological limits on juvenile survival, while the northern-offshore-spotted population is constrained by limits on adult survival.

As shown in Polacheck (1983), these two different constraints have different implications for the estimates of the input parameters. When the constraints are due to biological limits on juvenile survival rates (i.e. as for the spinner populations), one or more of the input parameters must be underestimated in order to obtain higher estimates of the net rate of growth. In contrast, when the results are constrained by an upper limit on adult survival rates (i.e. as in the northern-offshore-spotted population), one or more of the input parameters must be overestimated. Because the estimates of survival and net rate of increase respond in this manner to the input parameter, increases in the estimated ages at attainment of maturity for the spinner population and decreases in the estimated fecundity rate for the northern-offshore-spotted population would have the non-intuitive effect of increasing the estimated upper bound for the net rate of increase for these populations.

The net rates of increase derived from this method are inconsistent with current evaluations of the status of these stocks (Smith, 1983). Net rates of increase used in those evaluations ranged from 1.00 to 1.06, based in part on comparisons of gross reproductive rates. Moreover, a density-dependent response in the net rate of increase is assumed, so that the most exploited stock should have the highest net rate of increase. In contrast, the estimated net rate of increase in this paper only approaches 1.00 when the survival rates approach biologically unreasonable levels. In addition, the net rates of increase tend to be in an order the reverse of that to be expected under the concept of density-dependent response. Thus, the eastern-spinner population, which has been the most exploited, has the lowest rates, while the northern-whitebelly-spinner population, which is less exploited, tends to have the highest (Tables 2–4; and see Perrin and Henderson, 1984). If the current evaluations of the status of these stocks are correct, then the results from this method would suggest that the reproductive estimates used here are inconsistent with each other.

Before utilizing the results from this method in any specific application, the sensitivity of the estimates to both the assumptions of the methods and to the value of the input parameters needs to be considered. General conclusions about the sensitivity of this method are not possible, because the method as used here generates a range of estimates consistent with biological constraints on survival rates. The upper limits of this range are a complex, non-linear function of the input parameters. Even if this method is used to generate a single set of survival estimates by specifying the net rate of increase, the estimates will still be a non-linear function of the input parameters. For a specific set of input parameters, the sensitivity of the results can be explored by calculating estimates for a range of values consistent with possible sampling error and biases. Inclusion of such sensitivity analyses for the dolphin examples was beyond the scope of this paper. The sensitivity of the results to the values of input parameters for these dolphin populations is discussed in Polacheck (1983), where it is suggested that potential, but unknown, sampling biases (particularly in the estimates of the proportion mature) are the most likely factor to be affecting the results presented here.

In conclusion, as shown in this paper, reproductive data can be used to provide estimates for the range of survival rates and net rates of increases that are biologically reasonable and consistent. The method is not only useful for the estimates that it generates but also as a test of the consistency of a set of reproductive estimates and as a check of any independent set of estimates of survival rates and net rates of increase.

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Appendix

DERIVATION OF EQUATIONS 2 AND 3

For a stable age distribution:

$$N_i(t+1) = \lambda N_i(t) \tag{4}$$

where $N_i(t)$ = the number of individuals of age class i alive at time t and λ = the net rate of increase. Also from the projection matrix $\tilde{M}$

$$N_1(t+1) = N_{m+1}(t) \cdot F_A \tag{5}$$

$$N_i(t+1) = N_{i-1}(t) \cdot S_{i-1} \quad \text{for} \quad 1 < i \leqslant m \tag{6}$$

$$N_{m+1}(t+1) = N_{m+1}(t) \cdot S_A + N_m(t)\, S_m. \tag{7}$$

Note that $N_{m+1}(t)$ equals the number of adults alive at time t. Equating Equations 4 and 6 yields.

$$N_i(t) = (S_{i-1}/\lambda)\, N_{i-1}(t). \tag{8}$$

Beginning with age class 1, repeated applications of Equation 8 yield

$$N_i(t) = (S_j/\lambda)^{i-1}\, N_1(t) \quad \text{for} \quad 1 \leqslant i \leqslant m \tag{9}$$

since $S_i = S_j$ for $i = 1$ to $\tilde{m}$ and λ is a constant. Equating the right hand sides of Equations 4 (for $i = 1$) and 5 yields

$$N_1(t) = N_{m+1}(t)\, F_A/\lambda. \tag{10}$$

Substituting Equation 10 in Equation 9 yields

$$N_i(t) = (S_j/\lambda)^{i-1}\, (F_A/\lambda)\, N_{m+1}(t) \quad \text{for} \quad 1 \leqslant i \leqslant m. \tag{11}$$

Substituting the right hand side of Equation 11 in Equation 7 when $i = m$ and then equating the right hand sides of Equations 4 and 7 yields:

$$\begin{aligned} N_{m+1}(t+1) = \lambda N_{m+1}(t) &= N_{m+1}(t) \cdot S_A \\ &+ (S_j/\lambda)^{m-1}\, (F_A/\lambda)\, S_j N_{m+1}(t). \end{aligned} \tag{12}$$

Division of $\lambda N_{m+1}(t)$ and rearranging yields Equation 2. Equation 3 is derived by noting that from Equations 11 and 12, the total population size at time $t+1$ can be expressed as

$$\begin{aligned} \sum_{k-1}^{m+1} N_k(t+1) = &\sum_{i-1}^{m+1} (S_j/\lambda)^{i-1}\, F_A\, N_{m+1}(t) \\ &+ S_A\, N_{m+1}(t) \end{aligned} \tag{13}$$

Division of the right hand side of Equation 12 by the right hand side of Equation 13 yields Equation 3.

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AN OVERVIEW OF THE ECOPATH MODEL

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Recent trends in ecosystem modeling have produced complex simulation models which are very data intensive (Andersen and Ursin 1977; Laevastu and Larkins 1981). However, in many situations the construction of a biomass budget for a box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982; Polovina in press).

The ECOPATH model is an analytical procedure to estimate a biomass budget for a box model of an ecosystem given inputs which specify the components of the ecosystem, together with their mortality, diet, and energetics value. A computer program for ECOPATH has been written in BASIC-80, version 5.21, by Microsoft[1] (CP/M version) and a listing and users manual is available from the author.

The ECOPATH model produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the user specified species groups. The species groups represent aggregations of species with similar diet and life history characteristics and which have a common physical habitat. The ECOPATH model is not a simulation model with a time component as are some more complex ecosystem models. It estimates a biomass budget for the marine ecosystem in a static situation under the assumption that the ecosystem is at equilibrium conditions.

Equilibrium conditions are defined to exist when the mean annual biomass for each species group does not change from year to year. This condition results in a system of biomass budget equations which, for species group i, can be expressed as:

Production of biomass for species i - all predation on species i - nonpredatory biomass mortality for species i - fishery catch for species i = 0, for all i ...1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i's. The mean annual biomass estimates are obtained by solving the system of simultaneous linear equations.

ECOPATH requires the following input data:

A. The species groups or "boxes" of the ecosystem are to be specified by the user. These species groups are typically aggregates of species at the same trophic level with similar life history and population parameters. Species groups can be as restrictive as "tunas" or as aggregated as "pelagics" depending on the levels of detail of the following input data and intent of the user.

B. For each species group the following must be specified:

1. Annual production to biomass ratio (P/B). Where growth follows a von Bertalanffy curve, and mortality is negative exponential, the P/B value for many species groups is the annual

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

instantaneous mortality (Z) while for primary and secondary producers whose growth is more likely to be linear the P/B value can be taken to be the reciprocal of the mean age (Allen 1971).

2. Diet composition (DC). For a given species group this is the fraction, by weight, of each species group it consumes. These data typically are obtained from analysis of stomach contents (Macdonald and Green 1983).
3. Total annual food required (FR). This is the amount the average individual of a species group must consume annually as a multiple of the mean individual body weight.
4. Ecotrophic efficiency (EE). This is the fraction of total production removed annually by fishing and predation mortality. Typically in the range of 0.75-0.95 (Ricker 1969).
5. Habitat area (HA). The total area of habitat for each species group.
6. Annual fishery catch data (catch). The annual fishery yield for any species group for which there is substantial fishery mortality. If there is no fishery catch data then the mean annual biomass (B) for at least one species group must be inputed to insure that there is a unique solution to the set of biomass equations.

The ECOPATH model was applied to a coral reef ecosystem with 15 species groups. The output of ECOPATH simplified to 12 species groups was used to construct the biomass and production budget for the coral reef ecosystem given in Figure 1.

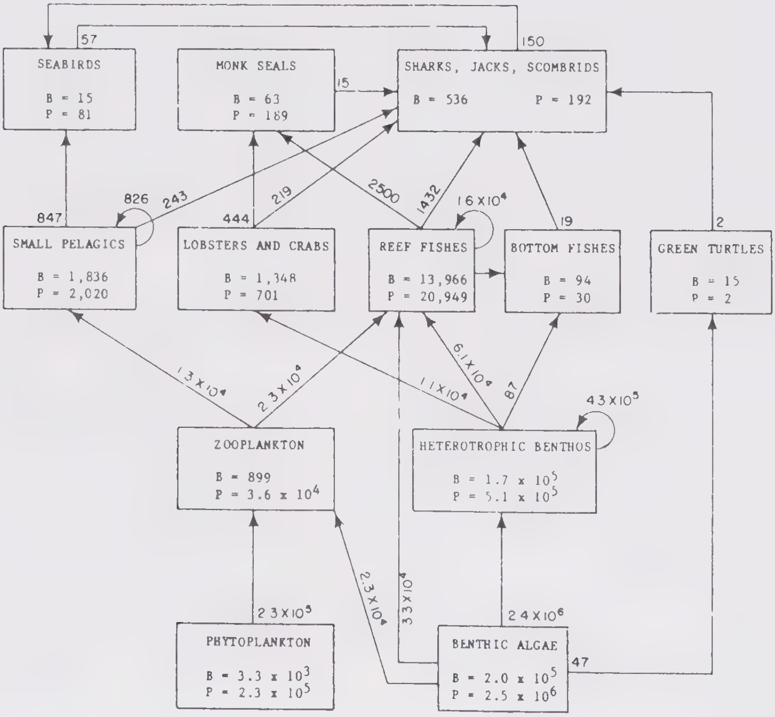
57
150
SEABIRDS
B = 15
P = 81
MONK SEALS
B = 63
P = 189
15
SHARKS, JACKS, SCOMBRIDS
B = 536
P = 192
826
243
219
2500
1432
1.6×10^4
847
444
19
2
SMALL PELAGICS
B = 1,836
P = 2,020
LOBSTERS AND CRABS
B = 1,348
P = 701
REEF FISHES
B = 13,966
P = 20,949
BOTTOM FISHES
B = 94
P = 30
GREEN TURTLES
B = 15
P = 2
1.3×10^4
2.3×10^4
6.1×10^4
1.1×10^4
87
4.3×10^5
ZOOPLANKTON
B = 899
P = 3.6×10^4
HETEROTROPHIC BENTHOS
B = 1.7×10^5
P = 5.1×10^5
2.3×10^5
2.3×10^4
3.3×10^4
2.4×10^6
47
PHYTOPLANKTON
B = 3.3×10^3
P = 2.3×10^5
BENTHIC ALGAE
B = 2.0×10^5
P = 2.5×10^6

Fig. 1. Biomass budget for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of kg/km^2 based on a habitat area of 1,200 km^2.

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ECOPATH - AN ECOSYSTEM MODEL APPLIED TO FRENCH FRIGATE SHOALS

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ABSTRACT

A simple model to estimate mean annual biomass, production, and consumption for components of an ecosystem is presented. The approach partitions the ecosystem into groups of similar species and requires estimates for these species groups of production to biomass, diet, and food consumption.

The approach was applied to an ecosystem at French Frigate Shoals in the Northwestern Hawaiian Islands where field work provided estimates of some of the input parameters as well as estimates of mean annual biomass and production, for some of the species groups modeled, to validate the estimates generated by the model. Simplified, the model depicts an ecosystem composed of four major trophic levels. The primary pro duction consists of benthic algae and phytoplankton, the second level is composed of zooplankton and heterotrophic benthos, the third level consists of reef fishes, lobsters, crabs, bottomfishes, and small pelagic species including squid, flyingfish, akule, and opelu, and the top trophic level is composed of sharks, jacks, tunas, seabirds, and monk seals.

Simple sensitivity analysis was performed to measure the sensitivity of the estimates of the model to errors or uncertainties in the input parameters.

biomass
ecosystem model
French Frigate Shoals
Northwestern Hawaiian Islands
tropical marine ecosystem

INTRODUCTION

The investigation of the resources of the Northwestern Hawaiian Islands (NWHI) is a multidisciplinary program with researchers from the National Marine Fisheries Service (NMFS), University of Hawaii Sea Grant College Program, U.S. Fish and Wildlife Service (FWS), and Hawaii Division of Aquatic Resources (Shomura, 1980) conducting studies on specific species which are important components of the marine ecosystem in the area. An ecosystem modeling project evolved out of a desire of many of the researchers to bring together common elements from the various research projects to form a quantitative picture of the entire marine ecosystem. Initially several existing ecosystem models were considered for application to the NWHI ecosystem, particularly the Prognostic Bulk Biomass (PROBUB) model (Laevastu and Larkins, 1981) developed for the Bering Sea and the Andersen and Ursin (1977) North Sea model. However, the models require a level of understanding which has not yet been achieved for a tropical ecosystem. Similar sentiments are expressed by Larkin and Gazey (1981):

> As in the case of the Bering Sea simulation, it seems reasonable to conclude that the North Sea model has little utility for multispecies fisheries management in tropical waters. To even construct a model at a comparable level of detail for tropical fish communities is at present impractical. Even if the data were available for estimating the several thousand parameters involved, it would take many years of observation and experiment to verify the utility of the model. It is also difficult to visualize what kind of experimental management might be adopted to test the validity of such a model.
>
> The moral, it seems, is to simplify....

Although neither the PROBUB model nor the Andersen and Ursin model seemed appropriate for modeling the NWHI ecosystem, given the current level of knowledge, much of the philosophy and approach, particularly in the PROBUB model, was applicable to the NWHI ecosystem. Hence, a simple ecosystem model, termed the ECOPATH model was developed.

The ECOPATH model partitions the ecosystem into species groups and, given a set of parameter estimates as inputs, produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the species groups. A species group is an aggregation of species with similar diet and life history characteristics and which has a common physical habitat. Computationally and conceptually the model is very simple. The mean annual biomass estimates are obtained from the solution of a system of simultaneous linear equations.

THE ECOPATH MODEL

The objective of the ECOPATH model is to estimate the mean annual biomass for each species group and produce a biomass budget for the ecosystem, all under the assumption of equilibrium conditions. Such conditions are defined to exist when the mean annual biomass for each species group does not change from year to year. This condition results in a system of biomass budget equations which, for species group i, can be expressed as:

Production of biomass for species i - all predation on species i - nonpredatory biomass mortality for species i = 0 for all i . (1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i's. The formulation of each term of the biomass budget equation is presented in detail below.

Biomass Production

Production (P) for a cohort of animals over a period of 1 year is defined as:

$$P = \int_0^1 N_t \frac{d}{dt} (w_t)\, dt$$

and mean annual biomass (B) for the cohort is defined as:

$$B = \int_0^1 N_t w_t dt$$

where

N_t is the number of animals and w_t the mean individual weight at time t.

Allen (1971) investigated the production to biomass (P:B) ratio for a cohort over a range of mortality and growth functions. For a number of mortality and growth functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species group which consists of n cohorts or species with instantaneous annual total mortality (Z_i) for cohort or species i, where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species group production

(P) is the sum of the cohort production (P_i) and can be expressed as:

$$P = \sum_{i=1}^{n} P_i = \sum_{i=1}^{n} Z_i B_i \ . \qquad (2)$$

Under the assumption that the Z_i's are all equal to say Z, then total species group production can be expressed as P = ZB, where B is the mean annual species group biomass.

Allen (1971) also showed that when growth in weight is linear for a range of mortality functions, the P:B ratio is equal to the reciprocal of the mean age. For a number of other growth and mortality functions the ratio of cohort P:B can be the reciprocal of the mean lifespan. Thus, for a range of growth and mortality functions, total species group production can be expressed as P = CB, where B is the mean annual species group biomass and C is a parameter. In the subsequent application of the ECOPATH model to an ecosystem where there is very little fishing mortality, the P:B ratio for fishes and crustaceans is taken as the annual instantaneous natural mortality (M), whereas the P:B ratio for primary and secondary producers whose growth is more likely to be linear rather than the von Bertalanffy is estimated as the reciprocal of the mean age.

Predation Mortality

Predation mortality is the fraction of the biomass of a species group which is consumed by all predators. The ECOPATH model computes this mortality in the same fashion as the PROBUB model. Two types of information are needed. First, the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i. The primary source of this information is the analysis of stomach contents. The second type of information needed to ascertain predation mortality is the food requirements of the predator. The PROBUB model expresses the total food required (R_i) by a species group (i) as:

$$R_i = b_i B_i + a_i P_i$$

where

B_i is the annual mean species biomass, P_i is the annual production of species group i, and a_i and b_i are parameters to be estimated from energetics studies. The component b_i B_i is the food required to maintain the biomass B_i, and the component a_i P_i is the food required to support the biomass production P_i (Laevastu and Larkins, 1981).

In the ECOPATH model the production of species group i is $P_i = C_i B_i$, so the food required for species group B_i is

$$R_i = b_i B_i + a_i P_i$$

$$= b_i B_i + a_i C_i B_i$$

$$= (b_i + a_i C_i)\ B_i \ .$$

Thus the amount of species group j consumed by predator species group i is given as:

$$R_i DC_{ij} = (b_i + a_i C_i)\ B_i DC_{ij} \ .$$

Nonpredation Mortality

All mortality attributable to causes other than predation such as fishing mortality, spawning mortality, and disease is considered together under the category of nonpredation mortality. In the ECOPATH model this is determined as a fraction (d_i) of the mean annual biomass B_i.

For n species groups the biomass budget equation (1) becomes a system of n simultaneous equations as follows:

$$C_1 B_1 - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{k1} - d_1 B_1 = 0$$

$$\vdots \qquad\qquad \vdots \qquad\qquad\qquad\qquad \vdots \qquad \vdots$$

$$C_i B_i - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{ki} - d_i B_i = 0$$

$$\vdots \qquad\qquad \vdots \qquad\qquad\qquad\qquad \vdots \qquad \vdots$$

$$C_n B_n - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{kn} - d_n B_n = 0 \ .$$

With input estimates for parameters C_i (usually M_i), b_i, a_i, DC_{ij}, and d for all i and j, this system of equations is a system of n simultaneous equations linear in the unknown B_i's. This system of equations can be expressed in matrix form as AB = 0, where A is an n x n matrix of coefficient, B is an n-dimensional vector of mean annual species group biomass, and 0 is the null vector. Typically the matrix A will be of full rank and will only have a trivial solution:

$B_i = 0$ for all i .

It is therefore necessary to provide an estimate of at least one of the species group biomass B_i before there exists a unique nontrivial set of B_i's which solves the biomass budget system.

The following is an application of the ECOPATH model to obtain estimates of biomass and production for the component of the marine ecosystem at French Frigate Shoals (FFS) in the NWHI.

FRENCH FRIGATE SHOALS

French Frigate Shoals is located at lat. 24°50'N, long. 166° 10'W, approximately midway along the chain of islands and banks comprising the NWHI. It is described by Bakus (1979) as a "crescent-shaped reef on a circular submerged platform about 18 mi in diameter (almost an atoll). The shoals form a large lagoon, bordered on one side by 12 sand islets (total area 56 acres) with a small rock pinnacle (La Perouse Pinnacle, ca. 1 acre) near the center of the platform. The highest elevation is generally 5 ft above sea level except for La Perouse Pinnacle (135 ft high)." The area is an important nesting ground for the green turtle, *Chelonia mydas*, various species of seabirds, and the Hawaiian monk seal, *Monachus schauinslandi*.

The ecosystem of interest to the model is the reef and nearshore community from shoreline to a depth of 365 m (200 fathoms). This habitat describes a circular area with a radius of approximately 20 km and a total area of approximately 1,200 km^2. The reef habitat in this region defined as the area from shoreline to 55 m (0 to 30 fathoms), consists of approximately 700 km^2.

Fifteen species groups have been identified as the major component of the ecosystem within the region down to the 365 m depth around FFS. These species groups which will subsequently be described in detail are seabirds, monk seals, tiger sharks, reef sharks, sea turtles, small pelagics, jacks, reef fishes, lobsters and crabs, bottomfishes, nearshore scombrids, benthic algae, heterotrophic benthos, zooplankton, and phytoplankton.

The parameters which are required as inputs to the ECOPATH model are (for each species group): the P:B ratio C_i (usually M_i), the energetic parameters a_i and b_i, the diet vector DC_{ij}, and the nonpredation mortality d_i. In addition, as discussed earlier, it is necessary to enter an estimate of at least one of the species group biomass values to have a nonzero solution to the biomass equations. The logical apex predator to drive the system is the tiger shark, *Galeocerdo cuviere*. However, in addition to the tiger shark biomass as a fixed input, biomass estimates for birds and monk seals will be treated as fixed inputs since they are based on visual censuses and are considered reliable.

Many of the estimates for input parameters are determined from field data collected at FFS. In some cases, however, data to estimate parameters were not available from FFS, or anywhere in the NWHI, so estimates from the literature were used. This was almost exclusively the case for the estimate of the nonpredatory mortality d_i. The d_i exclusive of fishery mortality used in a Gulf of Alaska simulator ranged from 0.019 to 0.029 (Livingston, 1977); thus a mean value of $d_i = 0.024$ was used in the ECOPATH model in the absence of any other information.

Typically the value C_i was estimated as annual instantaneous natural mortality (M_i) in the absence of fishing mortality. In some instances only von Bertalanffy growth parameters were estimated from field work and then M_i was estimated from a regression equation proposed by Pauly (1980) as:

$$\log_{10} M_i = 0.0066 - 0.279 \log_{10} L_i + 0.6543 \log_{10} K_i$$
$$+ 0.4634 \log_{10} T_i$$

where

L_i is the asymptotic maximum length (cm) of the stock, K_i the von Bertalanffy annual growth coefficient, and T_i the mean environmental temperature (°C) for the stock.

There is a shortage of energetics work on tropical stocks. Estimated food uptake for a temperate North Sea stock of cod based on a study of stomach contents suggests that the stock consumes an average of 0.75 percent of its body weight per day (Daan, 1973). For faster-growing fishes such as salmon, food consumption may be as high as 2.0 percent of its body weight per day (Laevastu and Larkins, 1981). Consumption relative to net production, or ecological efficiency, has been examined for a number of stocks and found to range from 10 to 25 percent (Crisp, 1975). Ecological efficiencies for three size groups of a Bermuda reef fish, *Epinephelus guttatus*, ranged from 15 to 25 percent (Menzel, 1960).

In the absence of any energetics input to estimate a_i and b_i, the value of b_i used was 2.0 from Laevastu and Larkins (1981). Since the amount of food needed for the maintenance of a species group i is b_iB_i, $b_i = 2.0$ implies that tbe species group must annually consume twice its biomass for maintenance. The food required to support production (P_i) is a_iP_i. In the absence of any food requirement information, a value of $a_i = 5$ was used, which, with the range of P:B values used in the model, results in ecological efficiencies and total consumption rates which are in agreement with the previously mentioned values.

Seabirds

Studies by the Fish and Wildlife Service indicate that the following seabirds are found in abundance at FFS: sooty tern, *Sterna fuscata*; black noddy, *Anous tenuirostris*; brown noddy, *A. stolidus*; great frigatebird, *Fregata minor*; red-footed booby, *Sula sula*; masked booby, *S. dactylatra*; wedge-tailed shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. nigripes*. An estimated peak population of 320,000 birds and a mean residence time of 6 months produce a mean annual seabird population estimated at 160,000 birds. Of this population 25 to 50 percent of the birds (mean individual weight of 0.31 kg) feed in the 1,200 km^2 area around FFS (Harrison et al., 1983). Thus, the estimated mean density for seabirds is 15.4 kg/km^2. Their diet composition vector is 0.68 small pelagics, 0.15 reef fishes, 0.10 jacks, 0.02 nearshore scombrids, and 0.05 zooplankton, and they consume an average of 80 times their biomass annually (Harrison et al., 1983).

Monk Seal

The second apex species is the Hawaiian monk seal. The estimate of biomass for the seal population in the 1,200 km^2 region around FFS, obtained from a visual census, is 75,500 kg, which results in a density of 63 kg/km^2 (W.G. Gilmartin, 1982: personal communication). The diet is estimated to consist of 0.85 reef fish and 0.15 lobster and crab, and it is estimated that the monk seal must consume on the average 45 times its weight in food per year to support growth and maintenance (W.G. Gilmartin, 1982: personal communication).

Tiger Shark

The tiger shark is the predominant apex predator at FFS. The stomach contents of 27 tiger shark suggest a diet vector consisting of 0.30 seabirds, 0.01 tiger shark, 0.28 reef fish, 0.01 turtles, 0.08 monk seal, 0.14 lobsters, 0.05 jacks, 0.08 small pelagics, 0.03 reef sharks, and 0.02 nearshore scombrids (DeCrosta, 1981). The tiger shark population at FFS is estimated at 504 individuals with a mean individual weight of 100 kg (DeCrosta, 1981). These values result in a density of 42 kg/km^2 for tiger shark biomass over the 1,200 km^2 area at FFS.

Reef Sharks

This is a group of nearshore warm-water sharks other than the tiger shark. Based on observations and catches at FFS, this group includes the gray reef shark, *Carcharhinus amblyrhynchos*, the galapagos shark, *C. galapagensis*, the small blacktip shark, *C. limbatus*, the sandbar shark, *C. milberti*, the dusky shark, *C. obscurus*, and the whitetip reef shark, *Triaenodon obesus*. They occur in greatest numbers in the deeper waters outside of the reef, but also work their way into the shallow waters of the inner reef. These sharks prey primarily on the smaller reef fishes, but their diet also includes pelagic fishes, bottom-dwelling fishes, stingrays, crustaceans, squid, and octopuses. Based on an analysis of stomach contents (DeCrosta, 1981), their diet is estimated as 0.90 reef fishes, 0.05 lobsters, and 0.05

jacks. Mortality estimates are not available for reef sharks in the NWHI. However, Holden (1977) presented estimates of annual instantaneous natural mortality for a number of shark species. These estimates generate a range of annual natural mortality from 0.1 to 0.25. The midpoint of this range 0.175 was used as an estimate of reef shark natural mortality and as the estimate of the P:B ratio.

Sea Turtle

This species group consists of the Hawaiian green sea turtle, _Chelonia mydas_. The diet of the green turtle is estimated at 0.90 benthic algae and 0.10 zooplankton (G.H. Balazs, 1982: personal communication). The annual instantaneous mortality is estimated at 0.15 and the annual food requirement for growth and maintenance is estimated at 22 times the mean annual biomass (G.H. Balazs, 1982: personal communication).

Small Pelagics

This group consists of small surface pelagic fishes and squid including flyingfish, Exocoetidae; opelu, _Decapterus_ spp.; akule, _Selar crumenophthalmus_, needlefish, Belonidae; and halfbeaks, Hemiramphidae. The bulk of the biomass for the group consists of akule, opelu, squid, and flyingfish. Based on a von Bertalanffy growth parameter of L_∞ = 27 cm and k = 0.215 for akule in Hawaii (Kawamoto, 1973), M = 0.65 was estimated. The growth parameters for opelu in Hawaii are estimated at L_∞ = 35 cm and k = 0.82 (Yamaguchi, 1953), resulting in an estimate of M = 1.50. An average value of M = 1.1 is used as the P:B ratio. The flyingfish, squid, akule, and opelu feed almost exclusively on zooplankton.

Jacks (carangids and large carnivores)

This is a group of active, fast-swimming carnivores including the white ulua, _Caranx ignobilis_; omilu, _C. melampygus_; ulua, _Carangoides ferdau_; and barracuda, _Sphyraena barracuda_. This group is found both in the reef and nearshore regions. Based on an analysis of stomach contents (Sudekum, 1981) it is estimated that their diet is 0.80 reef fish, 0.12 lobster and crab, and 0.08 small pelagics. Based on estimated growth parameter for _Seriola dumerili_ of L_∞ = 149 cm and k = 0.31 (J.H. Uchiyama, 1982: personal communication), M is estimated as 0.52 and this is used as the P:B estimate.

Reef Fishes (and octopuses)

This group consists primarily of the coral reef fishes, excluding the snappers, groupers, and carangids. Their habitat ranges from the surge zone down to depths of 55 m (30 fathoms).

Based on analysis of stomach contents from reef fishes collected at FFS, the diet is estimated at 0.17 zooplankton, 0.248 benthic algae, 0.459 heterotrophic benthos, and 0.123 reef fishes (J.D. Parrish, 1981: personal communication). Typically, members of this group have a relatively high natural mortality. For the kumu, *Parupeneus porphyreus*, the growth parameters are estimated at L_∞ = 49 cm and k = 0.54 (Moffitt, 1979) which yields an estimate of M = 1.0. The butterflyfish, *Chaetodon miliaris*, has growth parameters L_∞ = 12.7 cm and k = 1.13 (Ralston, 1976) which yields an estimate of M = 2.3. As a rather arbitrary average the value of M = 1.5 was used as the P:B estimate for this large reef fish species group.

Lobsters and Crabs

This group includes the spiny lobsters, *Panulirus marginatus* and *P. penicillatus*, the slipper lobster, *Scyllarides squammosus*, and various crabs including the kona crab, *Ranina ranina*. The M for the spiny lobster, *P. marginatus*, at FFS has been estimated from tagging studies as 0.32 for males and 0.71 for females (C. MacDonald, 1982: personal communication). An average value of M = 0.52 is taken as the P:B estimate for this group. The diet of this group is 100 percent heterotrophic benthos. Production and consumption rates were estimated for the spiny lobster, *P. homarus*, on a reef off South Africa by Berry and Smale (1980). They estimated the P:B ratio as 0.42, the production to consumption ratio as 0.45, and the consumption to biomass ratio as 9.5. To approximate these consumption and efficiency rates, the values of a = 2 and b = 12 were used in the food requirement equation.

Bottomfishes

This is a commercially important group of food fishes including opakapaka, *Pristipomoides filamentosus*; kalekale, *P. sieboldii*; gindai, *P. zonatus*; onaga, *Etelis coruscans*; ehu, *E. carbunculus*; uku, *Aprion virescens*; hapuupuu, *Epinephelus quernus*; kahala, *Seriola dumerili*, and butaguchi, *Pseudocaranx dentex*. Fishermen report that these bottomfishes are caught predominantly between depths of 75 and 220 m (40 and 120 fathoms). They are all active, carnivorous fishes which prey on small fish, shrimp and other crustaceans, and macrozooplankton.

Stomach contents were examined for the predominant species lex, and a mean diet vector for this group is estimated as 0.125 small pelagics, 0.469 reef fishes, 0.018 lobsters and crabs 0.026 bottomfishes, 0.104 zooplankton, and 0.258 heterotrophic benthos (S.V.D. Ralston, 1982: personal communication).

A detailed analysis of growth and mortality for the opakapaka, provided an estimate of M = 0.32 (Ralston, 1981). This mortality estimate is used for the bottomfish species group P:B estimate.

Nearshore Scombrids (and other carnivores)

This is a group of commercially important tunas and tunalike fishes, including skipjack tuna, Katsuwonus pelamis; kawakawa, Euthynnus affinis; yellowfin tuna, Thunnus albacares; wahoo, Acanthocybium solandri; dolphin, Coryphaena hippurus; and the rainbow runner, Elagatis bipinnulata. The members of this group are all pelagic or nearshore pelagic species which largely occupy the surface waters. The kawakawa, an inshore pelagic fish, has been observed foraging over the reefs in shallow water at FFS. These fishes are all active, fast-swimming carnivores and are opportunistic feeders. Their diets have been observed to consist predominantly of small fish, juvenile fish (tunas, snappers, carangids), squid, stomatopods, and megalops (Yoshida, 1979). Trolling from the RV Townsend Cromwell around FFS yielded 277 scombrids in 366 line-hours. The relative biomass catch vector for the 277 scombrids was 0.58 kawakawa, 0.27 wahoo, 0.12 yellowfin tuna, and 0.03 skipjack tuna. The diet for each of these fishes caught around Oahu based on analysis of stomach contents is presented in Tester and Nakamura (1957). An average diet vector weight by the relative biomass of each of these fishes yields a species group diet vector of 0.91 small pelagics and 0.09 zooplankton.

Preliminary estimates of growth parameters for kawakawa are $L_\infty = 58.0$ cm and $k = 0.42$ (J.H. Uchiyama, 1982: personal communication). The estimated $M = 0.66$ from these growth estimates served as the estimate of the P:B ratio.

Zooplankton (including fish larvae)

The P:B ratio for zooplankton is size-specific, ranging from 18 to 91 (J. Hirota, 1982: personal communication). The geometric mean for this range is 40, the value used for the P:B ratio. The zooplankton diet is 0.95 phytoplankton and 0.05 benthic algae.

Phytoplankton

Because the model is predator driven, the only parameter needed for phytoplankton is the P:B ratio which is estimated at 70 (J. Hirota, 1982: personal communication).

Heterotrophic Benthos

This group consists of all the invertebrates, bacteria, and protozoans living on the benthic substrate. The P:B ratio is estimated at 3.0 (J. Hirota, 1982: personal communication). The diet is 0.15 heterotrophic benthos and 0.85 benthic algae.

Benthic Algae

This group consists of fleshy algae, turf algae, and corals. The only parameter required for this species group is the P:B ratio which is estimated at 12.5 (J. Hirota, 1982: personal communication).

A summary of all the input parameter estimates are provided in Tables 1 and 2.

RESULTS AND DISCUSSION

The ECOPATH estimates of mean annual biomass and annual production for the species group at FFS are provided in Table 3 and a simplified ecosystem food web is schematically presented in Figure 1. As might be expected the reef fishes group is the largest in terms of biomass after the primary producers and heterotrophic benthos. The biomass and production for this group of reef fishes can be checked from current field studies on reef habitat and reef transects at FFS (H. Okamoto and Hobson, 1979: personal communication; R.W. Grigg and J.D. Parrish, 1979: personal communication). These studies suggest that 12 percent of the area from the 0 to 18 m (0 to 10 fathoms) depth is rich in reef fishes, 17 percent is moderate, and 71 percent is sparse. It is assumed that the area in depths from 18 to 55 m (10 to 30 fathoms) is entirely a sparse habitat. A total of 36 transects produced estimates of fish biomass as follows: for a rich habitat 163,666 kg/km^2; for a moderate habitat 16,815 kg/km^2; and for a sparse habitat 1,569.4 kg/km^2. This gives an average density of reef fishea at FFS of 15,000 kg/km^2 which compares with the model estimate of 24,163 kg/km^2 over the reef habitat. Production of fishes from a reef in Bermuda was estimated at 22,000 kg/km^2/yr (Bardach, 1959) which is also comparable with the model estimate of 36,244 kg/km^2/yr (Table 3).

Although an estimate of density for bottomfishes is not available to check the model value, an estimate for maximum sustainable yield (MSY) of bottomfishes at Penguin Bank in the Hawaiian Archipelago has been obtained based on the Schaefer surplus production model. The estimated MSY, which is a lower bound because it does not take into account a recreational fishery, is 272 kg/nmi of 100-fathom isobath (Ralston and Polovina, 1982). Using Gulland's formula MSY = 1/2 M B_o, with the value M = 0.32 used in the model and the model estimate of B_o = 387 kg/km^2, an estimated MSY of 62 kg/km^2 is obtained. Since the bottomfish habitat is approximately 300 km^2 and the length of the 100-fathom contour at FFS is 65 nmi, the estimated MSY of 62 kg/km^2 is equivalent to an MSY of 286 kg/nmi of 100-fathom isobath which is in agreement with the Penguin Bank value.

TABLE 1. DIET (PERCENTAGE BY SPECIES GROUP) OF SPECIES GROUPS AT FRENCH FRIGATE SHOALS

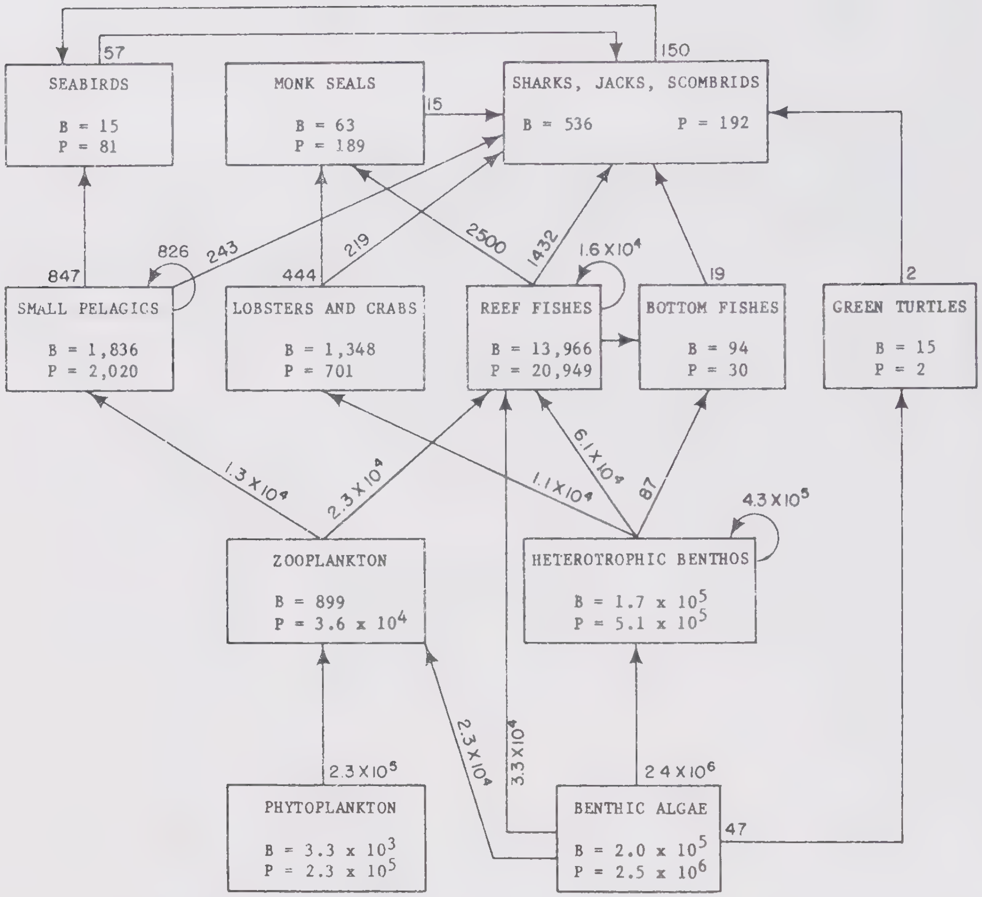
Birds	
Small pelagics	68
Jacks	10
Reef fishes	15
Nearshore scombrids	2
Zooplankton	5
Tiger sharks	
Birds	30
Monk seals	8
Tiger sharks	1
Reef sharks	3
Turtle	1
Small pelagics	8
Jacks	5
Reef fishes	28
Lobster and crabs	14
Nearshore scombrids	2
Small pelagics	
Small pelagics	6
zooplankton	94
Reef fishes	
Reef fishes	12.3
Zooplankton	17
Heterotrophic benthos	45.9
Benthic algae	24.8
Bottomfishes	
Small pelagics	12.5
Reef fishes	46.9
Lobsters and crabs	1.8
Bottom fishes	2.6
Zooplankton	10.4
Heterotrophic benthos	25.8
Monk seals	
Reef fishes	85
Lobsters and crabs	15
Reef sharks	
Small pelagics	5
Reef fishes	90
Lobsters and crabs	5
Turtles	
Zooplankton	10
Benthic algae	90
Jacks	
Small pelagics	8
Reef fishes	80
Lobsters and crabs	12
Lobsters and crabs	
Heterotrophic benthos	100
Nearshore scombrids	
Small pelagics	48
Reef fishes	8
Bottom fishes	8
Zooplankton	36
Heterotrophic benthos	
Heterotrophic benthos	15
Benthic algae	85
Zooplankton	
Phytoplankton	91
Benthic algae	9

TABLE 2. INPUT PARAMETERS FOR THE ECOPATH MODEL

Species Group	Production/ Biomass	Food for Production Biomass	Food for Maintenance Biomass	Nonpredatory Mortality	Biomass for Apex Species (kg/yr^2)
Birds	5.40	15	2	--	15.4
Monk seals	3.00	15	2	--	63.0
Tiger shark	0.25	10	2	--	42.0
Reef sharks	0.18	10	2	0.024	--
Turtles	0.15	10	2	0.024	--
Small pelagics	1.10	5	2	0.024	--
Jacks	0.47	5	2	0.024	--
Reef fishes	1.50	5	2	0.024	--
Lobsters and crabs	0.52	12	2	0.024	--
Bottom fishes	0.32	5	2	0.024	--
Nearshore scombrids	0.66	5	2	0.024	--
Zooplankton	40.00	7	2	0.024	--
Phytoplankton	70.00	--	--	0.024	--
Heterotrophic benthos	3.00	5	2	0.024	--
Benthic algae	12.50	--	--	0.024	--

TABLE 3. MEAN ANNUAL BIOMASS AND ANNUAL PRODUCTION ESTIMATE FROM ECOPATH MODEL

Species Group	Biomass Per Habitat Area (kg/km^2)	Annual Production Per Habitat Area (kg/km^2)	Habitat Area (km^2)	Ecological Efficiency (Production/ Consumption)	Consumption/ Biomass
Birds	15	83	1,200.00	0.07	83.0
Monk seals	63	189	1,200.00	0.06	47.0
Tiger sharks	42	11	1,200.00	0.06	4.5
Reef sharks	38	7	1,200.00	0.05	3.8
Turtles	15	2	1,200.00	0.04	3.5
Small pelagics	1,883	2,071	1,200.00	0.15	7.5
Jacks	421	147	1,200.00	0.09	3.8
Reef fishes	24,163	36,244	700.00	0.16	9.5
Lobsters and crabs	2,327	1,210	700.00	0.06	8.2
Bottom fishes	387	124	300.00	0.09	3.6
Nearshore scombrids	62	41	900.00	0.12	5.3
Zooplankton	912	36,486	1,200.00	0.14	282.0
Phytoplankton	3,345	234,157	1,200.00	0.00	0.0
Heterotrophic benthos	289,181	867,543	700.00	0.19	52.0
Benthic algae	342,598	4,282,471	700.00	0.00	0.0
Total biomass	390,604				
Total production		3,294,960			



SEABIRDS
B = 15
P = 81
MONK SEALS
B = 63
P = 189
SHARKS, JACKS, SCOMBRIDS
B = 536
P = 192
SMALL PELAGICS
B = 1,836
P = 2,020
LOBSTERS AND CRABS
B = 1,348
P = 701
REEF FISHES
B = 13,966
P = 20,949
BOTTOM FISHES
B = 94
P = 30
GREEN TURTLES
B = 15
P = 2
ZOOPLANKTON
B = 899
P = 3.6 x 10⁴
HETEROTROPHIC BENTHOS
B = 1.7 x 10⁵
P = 5.1 x 10⁵
PHYTOPLANKTON
B = 3.3 x 10³
P = 2.3 x 10⁵
BENTHIC ALGAE
B = 2.0 x 10⁵
P = 2.5 x 10⁶
57
150
15
826
243
219
2500
1432
1.6 X 10⁴
19
2
847
444
1.3 X 10⁴
2.3 X 10⁴
6.1 X 10⁴
1.1 X 10⁴
87
4.3 X 10⁵
2.3 X 10⁵
2.3 X 10⁴
3.3 X 10⁴
2.4 X 10⁶
47

Figure 1. Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of kg/km^2 based on a habitat area of 1,200 km^2 for purposes of trophic comparisons and will differ from estimates of B and P given in Table 3 when the habitat area is less than 1,200 km^2.

An estimate of the biomass of the reef shark population at FFS can be determined from population and mean weight estimates from DeCrosta (1981). The results of intensive fishing at FFS provide an estimate of the population of galapagos shark at 703 individuals and the gray reef shark at 826 individuals. With these population estimates and estimated mean weight of 60 kg for the galapagos shark and 20 kg for gray reef shark, the estimated biomass for the reef shark population is determined to be 48 kg/km^2. This compares with the model estimate of 38 kg/km^2. Hirota et al. (1980) estimated the primary production in the nearshore region in the NWHI at 670 metric tons (MT) biomass/km^2/yr. The model estimates that 234 MT/km^2/yr of phytoplankton production is needed to support life in the reef and nearshore ecosystem.

An estimate of net benthic primary production over a 700 km^2 habitat at French Frigate Shoals based on field measurements is 4.1 x 10^6 kg/km^2/yr (see expanded abstract in this proceedings by R. Grigg). The model estimates the net benthic algal production necessary to support the ecosystem at French Frigate Shoals at 4.3 x 10^6 kg/km^2/yr (Table 3).

The biomass of prey consumed by each predator is presented in Table 4. From Figure 1 and Table 4, it can be determined, for example, that monk seals consume most of the lobster and crab production but that they still constitute only a small portion of the monk seal diet compared with the portion of reef fishes.

SENSITIVITY ANALYSIS

To determine the sensitivity of the mean annual species group biomass estimated by the ECOPATH model to uncertainty or error in the inputted parameter estimates, a simple sensitivity analysis was performed. The set of input parameters used for the FFS biomass estimation served as the baseline values.

For a specific parameter, say the P:B value, the parameter for species group i was perturbed by a percentage p with all other parameters fixed at their baseline values, and the mean annual biomass for species group i was computed based on the perturbed parameter. The percentage of change of this new mean annual biomass from the baseline biomass for species group i was computed. This procedure was repeated for all i where each time the parameter for a new species group, say i + 1, was perturbed, the parameter value for species group i was returned to the baseline value. Let B_{io} represent the baseline mean annual biomass for species group i and B_{ip} represent the mean annual biomass for species group i when one of the input parameters was perturbed by p percent. Then a measure of the sensitivity of the estimate of mean annual biomass to a p percentage of change in a specific input parameter is the average absolute value of the change in mean annual biomass averaged over all species groups (avg B)

TABLE 4. PREDATOR CONSUMPTION VECTOR (KG/KM^2) BASED ON A HABITAT AREA 1,200 KM

Birds

Small pelagic	869
Jacks	128
Reef fishes	192
Nearshore scombrids	26
Zooplankton	64

Tiger sharks

Birds	57
Monk seals	15
Tiger sharks	2
Reef sharks	
Turtles	2
Small pelagics	15
Jacks	10
Reef fishes	53
Lobsters and crabs	27
Nearshore scombrids	4

Small pelagics

Small pelagics	847
Zooplankton	13,272

Reef fishes

Reef fishes	16,470
Zooplankton	22,763
Heterotrophic benthos	61,461
Benthic algae	33,208

Bottomfishes

Small pelagics	15
Reef fishes	163
Lobsters and crabs	6
Bottomfishes	9
Zooplankton	36
Heterotrophic benthos	90

Monk seals

Reef fishes	2,517
Lobsters and crabs	444

Reef sharks

Pelagics	7
Reef fishes	127
Lobsters and crabs	7

Turtles

Zooplankton	5
Benthic algea	47

Jacks

Small pelagics	126
Reef fishes	1,263

Lobster and crabs

Heterotrophic benthos	11,187

Nearshore scombrids

Small pelagics	117
Reef fishes	20
Bottomfishes	20
Zooplankton	88

Heterotrophic benthos

Heterotrophic benthos	260 x 10
Benthic algae	1.5 x 10

Zooplankton

Phytoplankton	234 x 10
Benthic algae	23 x 10

where

$$\text{avg B} = \sum_{i=1}^{15} |B_{io} - B_{ip}| / 15\ B_{io}\ .$$

Similarly the sensitivity of the estimated total ecosystem mean annual biomass (TB) to change in the input parameters can be measured by the average change in TB when a specific parameter is perturbed for one species group at a time. If TB_{ip} represents the total ecosystem mean annual biomass when a parameter for species group i is perturbed by p percent, and if TB is the total ecosystem mean annual baseline biomass, then a measure of the sensitivity of the total biomass to change in a single parameter is the average absolute change in total biomass (avg TB) where:

$$\text{avg TB} = \sum_{i=1}^{15} |TB - TB_{ip}| / 15\ TB\ .$$

The values of avg B and avg TB for changes in P:B, d, a, b, and the apex B's are given in Table 5. The estimate of mean annual biomass and total ecosystem biomass is relatively insensitive to change in the input parameters a, b, d, and the apex B's. For example, an increase in the value of a, the ratio of food required for growth, by 25 percent only results in a 1.8 per cent change in the average mean annual biomass and a 2.8 percent change in total biomass. However, the estimate of mean annual biomass is quite sensitive to changes in the P:B value. A 25 percent increase for a specific species group results in almost a 22 percent change in the average mean annual biomass, and a 25 percent decrease results in almost a 40 percent change. Fortunately, this sensitivity is restricted only to the species group for which the parameter is being perturbed since the average change in total ecosystem biomass is relatively small for the P:B parameter.

Thus far a parameter has been perturbed for only one species group at a time. The sensitivity of the estimated annual species group biomass and total ecosystem biomass to perturbation in the P:B value and food required (a and b together) for 10 percent changes in all species groups simultaneously is given in Table 6. Due to the prey-predator interactions a 10 percent change in all food consumption values or a 10 percent change in all P:B values can have a substantially greater effect on the estimated species group biomasses and the estimated total ecosystem biomass.

TABLE 5. AVERAGE CHANGE IN MEAN ANNUAL BIOMASS AND TOTAL ECOSYSTEM BIOMASS AS A FUNCTION OF CHANGE IN INPUT PARAMETERS

	Perturbation Relative to Baseline Value							
	0.75	0.80	0.85	0.90	1.10	1.15	1.20	1.25
				Parameter a				
avg B	0.016	0.013	0.010	0.006	0.007	0.011	0.014	0.018
avg TB	0.026	0.021	0.016	0.011	0.011	0.017	0.022	0.028
				Parameter b				
avg B	0.046	0.038	0.030	0.021	0.026	0.041	0.059	0.080
avg TB	0.049	0.040	0.031	0.021	0.024	0.038	0.053	0.070
				Parameter d				
avg B	0.014	0.011	0.008	0.006	0.006	0.009	0.012	0.015
avg TB	0.005	0.004	0.003	0.002	0.002	0.003	0.004	0.005
				P:B ratio				
avg B	0.394	0.292	0.204	0.127	0.101	0.144	0.183	0.219
avg TB	0.076	0.056	0.039	0.024	0.019	0.027	0.034	0.040
				Apex B's				
avg TB	0.083	0.067	0.050	0.033	0.033	0.050	0.067	0.083

TABLE 6. CHANGE IN MEAN ANNUAL BIOMASS AND TOTAL ECOSYSTEM BIOMASS AS A FUNCTION OF SIMULTANEOUS CHANGES IN A PARAMETER FOR ALL SPECIES GROUPS

	Perturbation Relative to Baseline Value	
	0.90	1.10
	Parameter Jointly a and b	
avg B	0.14	0.19
avg TB	0.23	0.32
	Parameter P:B	
avg B	0.25	0.17
avg TB	0.32	0.21

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This modeling work was a multidisciplinary project based on the research and expertise of a large number of researchers working on projects in the NWHI. The large numbers of references given as personal communication is because the model draws from research which is just being completed. I would particularly like to acknowledge Edward J. Webman who wrote the computer program for the ECOPATH model and Darryl T. Tagami who assisted during the early stages of this work.

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Model of a Coral Reef Ecosystem

I. The ECOPATH Model and Its Application to French Frigate Shoals

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Abstract. A simple model termed ECOPATH is presented which estimates mean annual biomass, production, and consumption for components of an ecosystem. To use the model, the ecosystem must be partitioned into groups of similar species and provide for these species groups, estimates of production to biomass, diet, and food consumption. The ECOPATH model is applied to an ecosystem at French Frigate Shoals in the Northwestern Hawaiian Islands. Extensive field work provides both estimates of the input parameters as well as estimates of mean annual biomass and production. Biomass and production estimates for some of the species groups modeled are used to validate the estimates generated by the model.

Introduction

In general, coral reefs have very high rates of gross primary production compared with other marine ecosystems (Odum and Odum 1955; Gordon and Kelly 1962; Ryther 1969; Lewis 1977). This characteristic is often considered to be a paradox since most coral reefs in the world occur at ocean latitudes characterized by nutrient poor waters (Muscatine and Porter 1977). Atolls in fact have been likened to oases in the desert. In answer to this apparent paradox, many workers have associated the high productivity found on coral reefs with a highly efficient mechanism that recycles nutrients within the system (Muscatine and Porter 1977). These considerations have led some biologists to conclude that reef ecosystems are in general nutrient limited.

Another widespread view about coral reefs is that because of their high productivity, they are potentially capable of supporting relatively high sustainable fishery yields (Marten and Polovina 1982). If the latter contention is true, this raises a question of why so many coral reef fisheries in the world are in serious decline (Johannes 1978). Irrespective of the cause, the common depletion of coral reef resources underlines the need to develop a better understanding of the structure and function of coral reef ecosystems and the development of better tools for their management.

In this paper these questions and problems are re-examined in detail. The approach has been to construct a mathematical ecosystem model, ECOPATH, for an entire coral reef ecosystem and then use the model to estimate its standing stock and production budget. The ECOPATH model operates from the top of the food chain down, using field estimates of the biomass of top carnivores as a starting point. One of the outputs of the model is the net primary production of the entire system necessary to support the biomass of major species complexes known to be present. A major strength of this approach is that the ecosystem model can be tested by providing an independent measure of primary productivity. This was done using standard methods for analyzing reef metabolic performance (Smith and Marsh 1973; Smith and Kinsey 1978; Kinsey 1979). The results and discussion of this work are reported in Parts II and III (Atkinson and Grigg 1984 b; Grigg et al. 1984).

The island selected for study is French Frigate Shoals (FFS) in the Hawaiian Archipelago. It is situated at lat. 24° N and long. 166° W, approximately midway in the archipelago. This island was chosen for the modeling study because of the large number of research projects conducted there as a result of the Northwestern Hawaiian Islands (NWHI) fisheries investigations, a large-scale multidisciplinary 5-year study of resources in the Hawaiian Archipelago (Grigg and Pfund 1980; Grigg and Tanoue 1984).

The study is divided into three parts. In Part I (this paper), the ECOPATH model is described in general and then applied specifically to the marine ecosystem at FFS. The results of this work produce estimates of mean annual biomass and annual production for all the components of the ecosystem and in particular, the minimum net primary productivity needed to support the ecosystem. In Part II of the paper, actual measures of gross and net primary productivity for the entire reef ecosystem at

FFS are presented and compared with data for reef ecosystems elsewhere in the world. In Part III of the paper, net values of measured primary productivity are contrasted to those predicted by the model, and possible causes of the difference are discussed. In Part III, interrelationships of the results of Part I and Part II are described, particular regarding factors limiting primary production and the effects of predation and nonpredation mortality on community regulation. Potential and actual fishery yields and implications regarding various management options that might maximize production are also discussed.

Portions of this study (Part I) appear in a proceedings volume of a symposium on the Northwestern Hawaiian Islands held in Honolulu, Hawaii on May 25–27, 1983 (Grigg and Tanoue 1984). Those sections of this manuscript which appear in Grigg and Tanoue (1984) are so indicated by a footnote. The proceedings volume is a technical report of the University of Hawaii with a limited distribution. Hence those sections which are necessary to fully describe the model and the parameter estimates, are included here for completeness and the convenience of the reader.

The ECOPATH Model [1]

There are a number of published examples of ecosystem models developed with the goal of simulating the dynamics of an exploited marine ecosystem (Parrish 1975; Andersen and Ursin 1977; Laevastu and Larkins 1981). Most of these models, however, require a level of understanding of the static and dynamic elements of an ecosystem which have not yet been achieved for tropical systems. In a review of the Bering Sea model developed by Laevastu and the North Sea model developed by Andersen and Ursin, Larkin and Gazey (1981) conclude:

"As in the case of the Bering Sea simulation it seems reasonable to conclude that the North Sea model has little utility for multispecies fisheries management in tropical water. To even construct a model at a comparable level of detail for tropical fish communities is at present impractical. Even if the data were available for estimating the several thousand parameters involved, it would take many years of observation and experimentation to verify the utility of the model. It is also difficult to visualize what kind of experimental management might be adopted to test the validity of such a model."

However, in many situations the construction of a biomass budget box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982). The goal of the mathematical modeling work at FFS was to estimate annual production and mean annual biomass for the major components of the coral reef ecosystem for a static situation under general equilibrium conditions. The mathematical model developed to construct the biomass box model for the ecosystem is termed "ECOPATH".

The ECOPATH model partitions the ecosystem into species groups and, given a set of parameter estimates as inputs, produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the species groups. A species group is an aggregation of species having common physical habitat, similar diet, and similar life history characteristics.

Equilibrium conditions exist when the mean annual biomass for each species group does not change from year to year. This condition results in a system of biomass budget equations which, for species group i, can be expressed as:

Production of biomass for species i – all predation on species i – nonpredatory biomass mortality for species $i=0$ for all i. (1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i's. The formulation of each term of the biomass budget equation is presented in detail below.

Biomass Production

Production (P) for a cohort of animals over 1 year is defined as:

$$P=\int_0^1 N_t \frac{d}{dt}(w_t)dt$$

and mean annual biomass (B) for the cohort is defined as:

$$B=\int_0^1 N_t w_t dt\,,$$

where N_t is the number of animals and w_t the mean individual weight at time t.

Allen (1971) has investigated the production to biomass (P/B) ratio for a cohort of fish over a range of mortality and growth functions. For a number of growth and mortality functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species group which consists of n cohorts or species and instantaneous annual total mortality (Z_i) for cohort or species i, where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species group production (P) is the sum of the cohort production (P_i) and can be expressed as:

$$P=\sum_{i=1}^{n} P_i=\sum_{i=1}^{n} Z_i B_i\,. \tag{2}$$

Under the assumption that the Z_i's are all equal to Z, then total species group production can be expressed as:

$$P=ZB$$

where B is the mean annual species group biomass.

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[1] Portions of this section also appear in Grigg and Tanoue (1984)

Allen (1971) has also shown that when growth in weight is linear for a range of mortality functions, the P/B ratio is equal to the reciprocal of the mean age. For a number of other growth and mortality functions, the ratio of cohort P/B can be the reciprocal of the mean lifespan. Thus, for a range of growth and mortality functions, total species group production can be expressed as:

$$P = C \cdot B,$$

where B is the mean annual species group biomass and C is a parameter. In the subsequent application of ECOPATH to an ecosystem where there is very little fishing mortality, the P/B ratio for fishes and crustaceans is taken as the annual instantaneous natural mortality (M), whereas the P/B ratio for primary and secondary producers whose growth is more likely to be linear rather than the von Bertalanffy, is estimated as the reciprocal of the mean age.

Predation Mortality

The predation mortality is the fraction of the biomass of a species group which is consumed by all predators. The ECOPATH model computes this mortality in the same fashion as the Laevastu's PROBUB model (Laevastu and Larkins 1981). Two types of information are needed. First, the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i. The primary source of this information is the analysis of stomach contents (Macdonald and Green 1983). The second type of information needed to ascertain predation mortality is the food requirements of the predator. The PROBUB model expresses the total food required (R_i) by a species group (i) as:

$$R_i = b_i B_i + a_i P_i$$

where B_i is the annual mean species biomass, P_i is the annual production of species group i, and a_i and b_i are parameters to be estimated from energetics studies. The component $b_i\, B_i$ is the food required to maintain the biomass B_i, and the component $a_i\, P_i$ is the food required to support the biomass production P_i (Laevastu and Larkins 1981).

In the ECOPATH model, the production of species group i is $P_i = C_i B_i$, so the food required for species group B_i is

$$\begin{aligned} R_i &= b_i B_i + a_i P_i \\ &= b_i B_i + a_i C_i B_i \\ &= (b_i + a_i C_i) B_i \end{aligned}$$

Thus, the amount of species group j consumed by predator species group i is given as:

$$R_i DC_{ij} = (b_i + a_i\, C_i)\, B_i DC_{ij}\,.$$

Nonpredation Mortality

All mortality attributable to causes other than predation such as fishing mortality, spawning mortality, and disease is considered together under the category of nonpredation mortality. Since the fishing mortality is negligible at FFS, in this application of ECOPATH, nonpredation mortality is determined as a fraction (d_i) of the mean annual biomass B_i (Laevastu and Larkins 1981).

For n species groups, the biomass budget equation (1) becomes a system of n simultaneous equations as follows:

$$\begin{array}{lllll} C_1 B_1 - & \sum_{k=1}^{n} (b_k + a_k C_k) B_k DC_{k1} & - d_1 B_1 & = 0 \\ \vdots & \vdots & \vdots & \vdots \\ C_i B_i - & \sum_{k=1}^{n} (b_k + a_k C_k) B_k DC_{ki} & - d_i B_i & = 0 \\ \vdots & \vdots & \vdots & \vdots \\ C_n B_n - & \sum_{k=1}^{n} (b_k + a_k C_k) B_k DC_{kn} & - d_n B_n & = 0\,. \end{array}$$

With input estimates for parameters C_i (usually M_i), b_i, a_i, DC_{ij}, and d_i for all i and j, this system of equations is a system of n simultaneous equations linear in the unknown B_i's. This system of equations can be expressed in matrix form as $AB = O$, where A is an $n \times n$ matrix of coefficient, B is an n-dimensional vector of mean annual species group biomass, and O is the null vector. Typically the matrix A will be of full rank and will have a trivial solution:

$$B_i = O \text{ for all } i\,.$$

It is therefore necessary to provide an estimate of at least one of the species group biomass B_i before there exists a unique nontrivial set of B_i's which solves the biomass budget system.

In an ecosystem where there is fishing mortality, fish catches can be used instead of an estimate of a species group biomass to insure a nontrivial solution to the biomass budget system. A computer program written in "BASIC" for a microcomputer to implement a generalized version of ECOPATH which can utilize fish catch data is available from the author.

The following is an application of ECOPATH model to obtain estimates of biomass and production for the major components of the marine ecosystem at FFS in the NWHI from shoreline to 365 M (200 fathoms).

French Frigate Shoals

French Frigate Shoals is described by Bakus (1979) as a "crescent-shaped reef on a circular submerged platform about 18 mi in diameter (almost an atoll). The shoals form a large lagoon, bordered on one side by 12 sand islets (total area 56 acres) with a small rock pinnacle (La Perouse Pinnacle, ca. 1 acre) near the center of the platform. The highest elevation is generally 5 ft above sea level except for La Perouse Pinnacle (135 ft high)." The area is an important nesting ground for the green turtle, *Che-*

lonia mydas (Linnaeus), various species of seabirds, and the Hawaiian monk seal, *Monachus schauinslandi* (Matschie).

The ecosystem of interest is the reef and nearshore community from shoreline to a depth of 365 m (200 fathoms). This habitat describes a circular area with a radius of approximately 20 km and a total area of approximately 1,200 km^2. The reef habitat in this region is defined as the area from shoreline to 55 m (0–30 fathoms) and is approximately 700 km^2.

Fifteen species groups were identified as the major components of the ecosystem within the region down to 365 m (200 fathoms) around FFS. These species groups described in detail below, are tiger sharks, monk seals, seabirds, reef sharks, sea turtles, small pelagics, jacks, reef fishes, lobsters and crabs, bottom fishes, nearshore scombrids, benthic algae, heterotrophic benthos, zooplankton, and phytoplankton.

The parameters which are required as inputs to the ECOPATH model are (for each species group): the P/B ratio C_i (usually M_i), the energetic parameters a_i and b_i, the diet vector DC_{ij}, and the nonpredation mortality parameter d_i. In addition, as discussed earlier, it is necessary to enter an estimate of at least one of the species group biomass values to have a nonzero solution to the biomass equations. The observed apex predator at FFS which drives the system is the tiger shark, *Galeocerdo cuvieri*. However, in addition to the tiger shark biomass as a fixed input, biomass estimates for birds and monk seals were treated as fixed inputs since these estimates are based on visual censuses and are considered reliable.

Many of the estimates for input parametes are determined from field data collected at FFS. For some groups, however, data to estimate parameters were not available from FFS, or anywhere in the NWHI, so parameter estimates from the literature were used. This was almost exclusively true for the estimate of the nonpredatory mortality d_i. The d_i exclusive of fishery mortality used in a Gulf of Alaska simulator ranged from 0.019 to 0.029 per year (Livingston 1977)[2] so a mean value of $d_i = 0.024$ was used in ECOPATH in the absence of any other information.

Typically the value C_i was estimated as annual instantaneous natural mortality (M_i) in the absence of fishing mortality. In some instances only von Bertalanffy growth parameters were estimated from field work and then M_i was estimated from a regression equation proposed by Pauly (1980):

$$\log_{10}M_i = 0.0066 - 0.279\log_{10}L_i + 0.6543\log_{10}K_i + 0.4634\log_{10}T_i$$

where L_i is the asymptotic maximum length (cm) of the stock, K_i the von Bertalanffy annual growth coefficient, and T_i the mean environmental temperature (°C) for the stock.

Little research has been done on trophic energetics of tropical stocks. Estimated food uptake for a temperate North Sea stock of cod, based on a study of stomach contents, suggests that the stock consumes an average of 0.75% of its body weight per day (Daan 1973). For faster growing fishes such as salmon, food consumption may be as high as 2.0% of its body weight per day (Laevastu and Larkins 1981). Consumption relative to net production, or ecological efficiency, has been examined for a number of stocks and found to range from 10 to 25% (Crisp 1975). Ecological efficiencies for three size groups of a Bermuda reef fish, *Epinephelus guttatus*, ranged from 15 to 25% (Menzel 1960).

In the absence of any energetics input to estimate a_i and b_i, the value of b_i used was 2.0 from Laevastu and Larkins (1981). Since the amount of food needed for the maintenance of a species group i is b_iB_i, $b_i = 2.0$ implies that the species group must annually consume twice its biomass for maintenance. The food required to support production (P_i)is a_iP_i. In the absence of any food requirement information, a value of $a_i = 5$ was used, which typically results in ecological efficiencies in the range of 10–25% for the model's P/B values.

Species Groups

Tiger Shark. The tiger shark is the predominant apex predator at FFS. The stomach contents of 27 tiger sharks indicate a diet vector consisting of 0.30 seabird, 0.01 tiger shark, 0.28 reef fish, 0.01 turtle, 0.08 monk seal, 0.14 lobster, 0.05 jack, 0.08 small pelagics, 0.03 reef shark, and 0.02 nearshore scombrids (DeCrosta 1981). Respirometry studies suggest that on the average tiger sharks consume about 4.5 times their weight per year (DeCrosta 1981). The tiger shark population at FFS is estimated at 504 individuals; the mean individual weight is 100 kg (DeCrosta 1981). These values result in a density of 42 kg/km^2 for tiger shark biomass over the 1,200 km^2 area at FFS.

Monk Seal. Another apex species is the Hawaiian monk seal. The diet of the monk seal is estimated to be 0.85 reef fish and 0.15 lobster and crab, and it is estimated that the monk seal must consume, on the average, 45 times their weight in food per year to support growth and maintenance (WG Gilmartin, personal communication 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The estimate of biomass for the seal population in the 1,200 km^2 region around FFS is 75,500 kg obtained from a visual census, which results in a density of 63 kg/km^2 (WG Gilmartin, personal communication).

Seabirds. Studies by the U.S. and Wildlife Service indicate that the following seabirds are abundant at FFS: sooty tern, *Sterna fuscata*; black noddy, *Anous tenuirostris*; brown noddy, *A. stolidus*; great frigatebird, *Fregata*

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[2] Livingston P (1977) Numerical evaluation of marine biomasses in Gulf of Alaska (Evaluation of minimum sustainable biomasses of fisheries resources in the Gulf of Alaska using the Laevastu-Favorite bulk biomass model). Northwest and Alaska Fisheries Center, Natl Mar Fish Serv, NOAA, Seattle, WA 98112. Processed Report, 61 pp

minor; red-footed booby, *Sula sula*; masked booby, *S. dactylatra*; wedgetailed shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. niaripes*. An estimated peak population of 320,000 birds and a mean residence time of 6 months produce a mean annual seabird population estimated at 160,000 birds. Of this population, 25–50% of the birds (mean individual weight of 0.31 kg) feed in the 1,200 km^2 area around FFS (Harrison et al. 1983). Thus, the estimated mean density for seabirds is 15.4 kg/km^2. Their diet composition vector is 0.68 small pelagics, 0.15 reef fish, 0.10 jack, 0.02 nearshore scombrids, and 0.05 zooplankton, and they consume an average of 80 times their biomass annually (Harrison et al. 1983).

Reef Sharks. This is a group of nearshore warm water sharks other than the tiger shark. Based on observations and catches at FFS, this group includes the gray reef shark, *Carcharhinus amblyrhynchos*, the Galapagos shark, *C. galapagensis*, the small blacktip shark, *C. limbatus*, the sandbar shark, *C. milberti*, the dusky shark, *C. obscurus*, and the whitetip reef shark, *Triaenodon obesus*. They occur in greatest numbers in the deeper waters outside of the reef, but are also in the shallow waters of the inner reef. These sharks prey primarily on the smaller reef fishes, but their diet also includes pelagic fishes, bottom-dwelling fishes, stingrays, crustaceans, squids, and octopuses. Based on an analysis of stomach contents (DeCrosta 1981), we estimate their diet as: 0.90 reef fish, 0.05 lobster, and 0.05 jack. Mortality estimates are not available for reef sharks in the NWHI. However, Holden (1977) presents estimates of annual instantaneous natural mortality for a number of shark species. These estimates generate a range of annual natural mortality from 0.1 to 0.25. The midpoint of this range 0.175 was used as an estimate of reef shark natural mortality and as the estimate of the P/B ratio.

Sea Turtle. This species group consists of the green turtle. The diet of the green turtle is estimated at 0.90 benthic algae and 0.10 zooplankton (G. H. Balazs, personal communication 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The annual instantaneous mortality is estimated at 0.15 and the annual food requirement for growth and maintenance is estimated at 22 times the mean annual biomass (G. H. Balazs personal communication).

Small Pelagics. This group consists of small surface pelagic fishes and squid including flyingfish, Exocoetidae, opelu, *Decapterus* spp., akule, *Selar crumenophthalmus*, needlefish, Belonidae, and halfbeaks, Hemiramphidae. The bulk of the biomass for the group consists of akule, opelu, squid, and flyingfish. Based on a von Bertalanffy growth parameter of $L_\infty = 27$ cm and $k = 0.215$ for akule in Hawaii (Kawamoto 1973), $M = 0.65$ was estimated. The growth parameters for opelu in Hawaii are estimated at $L_\infty = 35$ cm and $k = 0.82$ (Yamaguchi 1953) resulting in an estimate of $M = 1.50$. An average value of $M = 1.1$ is used at the P/B ratio. The flyingfish, squid, akule, and opelu feed almost exclusively on zooplankton.

Jacks (Carangids and Large Carnivores). This is a group of active, fast-swimming carnivores including the white ulua, *Caranx ignobilis*; omilu, *C. melampygus*; ulua, *Carangoides ferdau*; and barracuda, *Sphyraena barracuda*. This group is found both within the reef and nearshore regions. Based on an analysis of stomach contents (Sudekum 1983), it is estimated that their diet is 0.80 reef fish, 0.12 lobster and crab, and 0.08 small pelagics. Based on estimated growth parameter for *Caranx melampygus* of $L_\infty = 91.7$ cm, $k = 0.22$ (Sudekum 1983), M is estimated as 0.47 and this is used as the P/B estimate.

Reef Fishes (Reef Fishes and Octopuses). This group consists primarily of the coral reef fishes, excluding the snappers, groupers, and carangids. Their habitat ranges from the surge zone down to depths of 55 m (30 fathoms).

Based on analysis of stomach contents from reef fishes collected at FFS, the diet is estimated at 0.17 zooplankton, 0.248 benthic algae, 0.459 heterotrophic benthos, and 0.123 reef fish (J. D. Parrish, personal communication 1981. Hawaii Cooperative Fishery Research Unit, University of Hawaii, Honolulu, HI 96822). Typically, members of this group have a relatively high natural mortality. For the kumu, *Parupeneus porphyreus*, the growth parameters are estimated at $L_\infty = 49$ cm and $k = 0.54$ (Moffitt 1979) which yields an estimate of $M = 1.0$. The butterflyfish, *Chaetodon miliaria* has growth parameters $L_\infty = 12.7$ cm and $k = 1.13$ (Ralston 1976) which yields an estimate of $M = 2.3$. Natural mortality estimates for six reef fish species from the Families Mugilidae, Mullidae, Blennidae, and Balistidae range from 0.31 to 2.60 (Pauly 1980). The value of $M = 1.5$ is taken as a mean for the reef fishes group and is used as the P/B estimate.

Lobsters and Crabs. This group includes the spiny lobsters, *Panulirus marginatus* and *P. penicillatus*, the slipper lobster, *Scyllarides squammosus*, and various crabs including the kona crab, *Ranina ranina*. The M for *P. marginatus* at FFS has been estimated from tagging studies as 0.32 for males and 0.71 for females (MacDonald 1984). An average value of $M = 0.52$ is taken as the P/B estimate for this group. The diet of this group is 0.98 heterotrophic benthos and 0.02 zooplankton. Production and consumption rates were estimated for the spiny lobster, *P. homarus*, on a reef off South Africa (Berry and Smale 1980). They estimated the P/B ratio as 0.42, the production to consumption ratio as 0.45, and the consumption to biomass ratio as 9.5. To approximate these consumption and efficiency rates, the values of $a = 2$ and $b = 12$ were used in the food requirement equation.

Bottom Fishes. This is a commercially important group of food fishes including opakapaka, *Pristipomoides fila-*

Table 1. Diet of species groups at French Frigate Shoals as a percentage of total diet

Birds	
Small pelagics	68
Jacks	10
Reef fishes	15
Nearshore scombrids	2
Zooplankton	5
Tiger sharks	
Birds	30
Monk seals	8
Tiger shark	1
Reef sharks	3
Turtles	1
Small pelagics	8
Jacks	5
Reef fishes	28
Lobsters and crabs	14
Nearshore scombrids	2
Small pelagics	
Small pelagics	6
Zooplankton	94
Reef fishes	
Reef fishes	12.3
Zooplankton	17
Heterotrophic benthos	45.9
Benthic algae	24.8
Bottom fishes	
Small pelagics	12.5
Reef fishes	46.9
Lobsters and crabs	1.8
Bottom fishes	2.6
Zooplankton	10.4
Heterotrophic benthos	25.8
Monk seals	
Reef fishes	85
Lobsters and crabs	15
Reef sharks	
Small pelagics	5
Reef fishes	90
Lobsters and crabs	5
Turtles	
Zooplankton	10
Benthic algae	90
Jacks	
Small pelagics	8
Reef fishes	80
Lobsters and crabs	12
Lobsters and crabs	
Heterotrophic benthos	98
Zooplankton	2
Nearshore scombrids	
Small pelagics	48
Reef fishes	8
Bottom fishes	8
Zooplankton	36
Heterotrophic benthos	
Heterotrophic benthos	15
Benthic algae	85
Zooplankton	
Phytoplankton	91
Benthic algae	9

mentosus; kalekale, *P. sieboldii*; gindai, *P. zonatus*; onaga, *Etelis coruscans*; ehu, *E. carbunculus*; uku, *Aprion virescens*; hapuupuu, *Epinephelus quernus*; kahala, *S. dumerili*; and butaguchi, *Pseudocaranx dentex*. Fishermen report that these bottom fishes are caught predominantly between 75 and 220 m (40 and 120 fathoms). They are all active, carnivorous fishes which prey on small fish, shrimp, and other crustaceans, and macrozooplankton.

Stomach contents have been examined for the predominant species in this multispecies complex, and mean diet vectors for this group are estimated to be 0.125 small pelagics, 0.469 reef fish, 0.018 lobster and crab, 0.026 bottom fish, 0.104 zooplankton, and 0.258 heterotrophic benthos (S. Ralston, personal communication January 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812).

A detailed analysis of growth and mortality for the opakapaka provided an estimate of $M = 0.32$ (Ralston 1981) which is used for the bottom fish species group P/B estimate.

Nearshore Scombrids (Nearshore Scombrids and Other Carnivores). This is a group of commercially important tunas and tunalike fishes, including skipjack tuna, *Katsuwonus pelamis*; kawakawa, *Euthynnus affinis*; yellowfin tuna, *Thunnus albacares*; wahoo, *Acanthocybium solandri*; dolphin, *Coryphaena hippurus*, and the rainbow runner, *Elagatis bipinnulata*. The members of this group are all pelagic or nearshore pelagic species which largely occupy the surface waters. The kawakawa is an inshore pelagic fish and has been observed foraging over the reefs in shallow water at FFS. These fishes are all active, fast-swimming carnivores, and are opportunistic feeders. Their diets have been observed to consist predominantly of small fish, juvenile fish (tunas, snappers, carangids), squid, stomatopods, and megalops (Yoshida 1979). Trolling from the RV *Townsend Cromwell* around FFS produced 277 scombrids in 366 line-hours. The relative biomass catch vector for the 277 scombrids was 0.58 kawakawa, 0.27 wahoo, 0.12 yellowfin tuna, and 0.03 skipjack tuna. The diet for each of these fishes caught around Oahu, based on analysis of stomach contents, is presented in Tester and Nakamura (1957). An average diet vector weight by the relative biomass of each of these fishes yields species group diet vectors of 0.91 for small pelagics and 0.09 for zooplankton.

Preliminary estimated growth parameters for kawakawa are $L_\infty = 118$ cm and $k = 0.42$ (J.H. Uchiyama, personal communication August 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The estimated $M = 0.66$ from these growth estimates served the estimate of the P/B ratio.

Zooplankton. This group includes fish larvae. The P/B ratio for zooplankton is size specific ranging from 18 to 91 (Crisp 1975). The geometric mean for this range is 40 and is the value taken for the P/B ratio. The zooplankton diet in 0.91 phytoplankton and 0.01 benthic algae.

Phytoplankton. Because the model in predator driven, the only parameter needed for phytoplankton is the P/B ratio which is estimated at 70 (Parsons and Takahashi 1973; Crisp 1975).

Heterotrophic Benthos. This group consists of all the benthic invertebrates. The P/B ratio for this species group is estimated at 3.0. The diet vector is 0.15 heterotrophic benthos and 0.85 benthic algae (Crisp 1975).

Benthic Algae. This group consists of fleshy algae, turf algae, and corals. The only parameter required for this species group is the P/B ratio which is estimated at 12.5 (Odum and Odum 1955).

A summary of all the input parameter estimates is provided in Tables 1 and 2.

Table 2. Input parameters for the tropical ecosystem biomass budget model

Species group	Production/ biomass (C_i)	Food for production biomass (a_i)	Food for maintenance biomass (b_i)	Nonpredatory mortality (d_i)	Biomass for apex species (B_i)
Tiger shark	0.25	10	2	–	42.0
Birds	5.4	15	2	–	15.0
Monk seals	3.0	15	2	–	63.0
Reef sharks	0.18	10	2	0.024	–
Turtles	0.15	10	2	0.024	–
Small pelagics	1.10	5	2	0.024	–
Jacks	0.47	5	2	0.024	–
Reef fishes	1.5	5	2	0.024	–
Lobsters and crabs	0.52	12	2	0.024	–
Bottom fishes	0.32	5	2	0.024	–
Nearshore scombrids	0.66	5	2	0.024	–
Zooplankton	40	7	2	0.024	–
Phytoplankton	70	–	–	0.024	–
Heterotrophic benthos	3.0	5	2	0.024	–
Benthic algae	12.5	–	–	0.024	–

Table 3. Mean annual biomass and annual production estimate from tropical ecosystem biomass budget model

Species group	Biomass per habitat area (kg/km^2)	Annual production per habitat area (kg/km^2)	Habitat area (km^2)	Ecological efficiency (production/ consumption)	Consumption/ biomass
Tiger shark	42	11	1,200.00	0.06	4.5
Monk seals	63	189	1,200.00	0.06	47.0
Birds	15	81	1,200.00	0.07	83.0
Reef sharks	38	7	1,200.00	0.05	3.8
Turtles	15	2	1,200.00	0.04	3.5
Small pelagics	1,836	2,020	1,200.00	0.15	7.5
Jacks	411	144	1,200.00	0.09	3.8
Reef fishes	23,941	35,912	700.00	0.16	9.5
Lobsters and crabs	2,311	1,202	700.00	0.06	8.2
Bottom fishes	377	121	300.00	0.09	3.6
Nearshore fishes	60	40	900.00	0.12	5.3
Zooplankton	899	35,944	1,200.00	0.14	282.0
Phytoplankton	3,295	230,679	1,200.00	0.00	0.0
Heterotrophic benthos	289,181	867,543	700.00	0.19	17.0
Benthic algae	342,598	4,282,471	700.00	0.00	0.0
Total biomass (kg/km^2)	390,604				
Total production (kg/km^2)		3,294,960			

Results[3]

The estimates of mean annual biomass and annual production for the species groups at FFS generated by the ECOPATH model are provided in Table 3, a food web based on the diet vector is given in Table 4, and a simplified ecosystem food web is schematically presented in Fig. 1. As might be expected, the reef fishes represent the largest biomass after the primary producers and heterotrophic benthos. The estimated mean reef fish biomass was 15,000 kg/km^2 over 700 km^2 area of reef fish habitat at FFS (Okamoto and Kanenaka 1983) which compares with the model estimate of 23,941 kg/km^2 (Table 3). Production of reef fishes from a reef in Bermuda was estimated at 22,000 kg/km^2/year (Bardach 1959) compared with the model's estimate of 35,912 kg/km^2/year (Table 3).

Although we do not have any estimates of density for deep bottom fishes to check the model value, an estimate for maximum sustainable yield (MSY) of bottom fishes at Penguin Bank in the Hawaiian Archipelago has been obtained based on the Schaefer surplus production model. The estimated MSY, which is a lower bound because it does not take into account a recreational fishery, is 272 kg/nautical mile (nmi) of 183-m (100-fathom) isobath

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[3] Portions of this section also appear in Grigg and Tanoue (1984)

(Ralston and Polovina 1982). Using Gulland's formula MSY $= 1/2\ M\ B_o$, with the value $M = 0.32$ used in the model and the estimate of $B_o = 387$ kg/km² produced by the model, an estimated MSY of 62 kg/km² is obtained. Since the bottom fish habitat is approximately 300 km² and the length of the 183-m (100-fathom) contour at FFS is 65 nmi, the estimated MSY of 62 kg/km² can be converted to an MSY of 286 kg/nmi of 183-m (100-fathom) isobath which is in close agreement with the Penguin Bank value.

An estimate of the biomass of reef shark populations at FFS can be determined from population and mean weight estimates from DeCrosta (1981). The results of intensive fishing at FFS provide an estimate of the Galapagos shark population at 703 individuals and the gray reef shark population at 826 individuals. With these population estimates and estimated mean weight for the Galapagos shark of 60, and 20 kg for gray reef shark, the estimated biomass for the reef shark population is 48 kg/km². This compares with the model estimate of 38 kg/km².

Hirota et al. (1980) estimated the primary production in the nearshore region of the NWHI at 900 metric tons (MT) biomass/km²/year. The model estimates that 234 MT/km²/year of phytoplankton production is needed to support the reef and nearshore ecosystem.

Net benthic primary production over a 700 km² habitat at FFS has been estimated to be 4.1×10^6 kg/km²/year (see Atkinson and Grigg 1984a). The ECOPATH model estimates the net benthic algal and coral primary production necessary to support the ecosystem at 4.3×10^6 kg/km²/year (Table 3).

Table 4. Predator consumption vector (kg/km²) based on a habitat area 1,200 km²

Birds		*Monk seals*	
Small pelagic	847	Reef fishes	2,517
Jacks	125	Lobsters and crabs	444
Reef fishes	187	*Reef sharks*	
Nearshore scombrids	25	Pelagics	7
Zooplankton	62	Reef fishes	127
Tiger sharks		Lobsters and crabs	7
Birds	57	*Turtles*	
Monk seals	15	Zooplankton	5
Tiger shark	2	Benthic algae	47
Reef sharks	6	*Jacks*	
Turtles	2	Small pelagics	123
Small pelagics	15	Reef fishes	1,233
Jacks	10	Lobsters and crabs	185
Reef fishes	53	*Lobster and crabs*	
Lobsters and crabs	27	Heterotrophic benthos	10,875
Nearshore scombrids	4	Zooplankton	233
Small pelagics		*Nearshore scombrids*	
Small pelagics	826	Small pelagics	115
Zooplankton	12,943	Reef fishes	19
Reef fishes		Bottom fishes	19
Reef fishes	16,319	Zooplankton	86
Zooplankton	22,555	*Heterotrophic benthos*	
Heterotrophic benthos	60,899	Heterotrophic benthos	4.3×10^5
Benthic algae	32,904	Benthic algae	2.4×10^6
Bottom fishes		*Zooplankton*	
Small pelagics	43	Phytoplankton	2.3×10^5
Reef fishes	160	Benthic algae	2.3×10^4
Lobsters and crabs	6		
Bottom fishes	9		
Zooplankton	36		
Heterotrophic benthos	87		

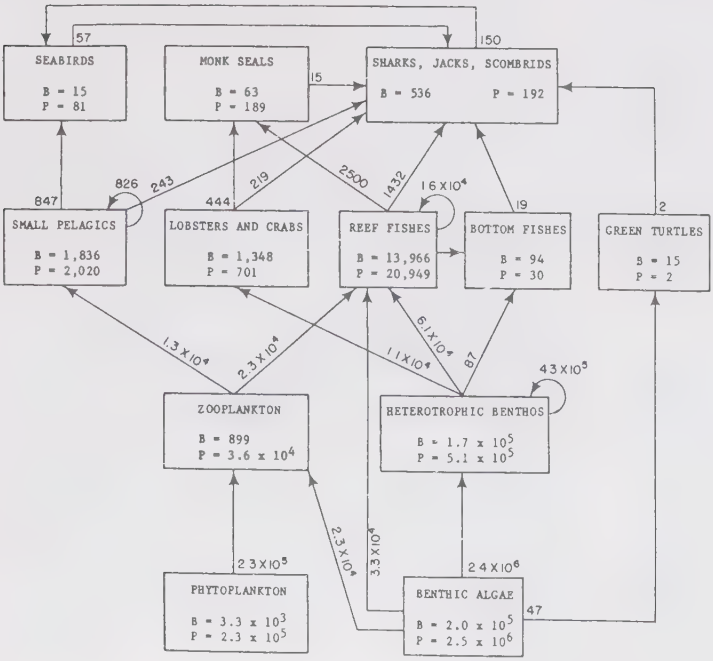
57
150
SEABIRDS
B = 15
P = 81
MONK SEALS
B = 63
P = 189
15
SHARKS, JACKS, SCOMBRIDS
B = 536
P = 192
826
243
219
2500
1432
16 X 10⁴
847
444
19
2
SMALL PELAGICS
B = 1,836
P = 2,020
LOBSTERS AND CRABS
B = 1,348
P = 701
REEF FISHES
B = 13,966
P = 20,949
BOTTOM FISHES
B = 94
P = 30
GREEN TURTLES
B = 15
P = 2
1.3 X 10⁴
2.3 X 10⁴
6.1 X 10⁴
1.1 X 10⁴
87
43 X 10⁵
ZOOPLANKTON
B = 899
P = 3.6 x 10⁴
HETEROTROPHIC BENTHOS
B = 1.7 x 10⁵
P = 5.1 x 10⁵
2.3 X 10⁴
3.3 X 10⁴
2 3 X 10⁵
2 4 X 10⁶
PHYTOPLANKTON
B = 3.3 x 10³
P = 2.3 x 10⁵
BENTHIC ALGAE
B = 2.0 x 10⁵
P = 2.5 x 10⁶
47

Fig. 1. Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of kg/km² based on a habitat area of 1,200 km²

The biomass of prey consumed by each predator is presented in Table 4. It can be determined from Fig. 1 and Table 4 that monk seals, for example, consume most of the lobster and crab production but that lobsters and crabs still constitute a small portion of the monk seal diet compared with their consumption of reef fishes.

Discussion

A schematic of the major prey-predator pathways for the ecosystem at FFS together with the model's estimate of mean annual biomass and annual production is presented in Fig. 1. The estimates of mean annual biomass and annual production in Fig. 1 are all normalized over a total habitat of 1,200 km^2 to facilitate estimation of trophic efficiencies. Hence in Table 3 net benthic primary production, for example, is 4.3×10^6 kg/km^2/year over its habitat of 700 km^2 while when this value is adjusted or normalized to the total 1,200 km^2 habitat for Fig. 1 it becomes 2.5×10^6 kg/km^2/year. From Fig. 1 the ratio of production from the zooplankton and heterotrophic benthos to primary production is 0.20. The ratio of production from the third level in Fig. 1, to zooplankton and heterotrophic benthos is 0.04. The ratio of production from the top level to that from the third level of Fig. 1 is 0.02. At first glance it would appear that these last two ratios do not conform to the usual range of ecological efficiencies which are in the order of 0.1 to 0.25 for these organisms (Steele 1974; Crisp 1975). However, the reason the values computed from Fig. 1 are low is that the levels in Fig. 1 do not represent single trophic levels as indicated by the arrows originating and ending in the same box for the small pelagics, reef fishes, and heterotrophic benthos species. If only the net production leaving one level and going to the level above is used as the denominator to compute the previous ratios, then the ratio of production at the second level to primary production is still 0.20, whereas the ratio of production from the third level to net production from the second level becomes 0.20, and the ratio of production from the top level to the net production from the second level becomes 0.08.

The high internal predation in the reef fishes group and the heterotrophic benthos group which is required by the diet composition inputs suggests that each of these groups probably represents two trophic levels. Under the assumption of two trophic levels within the reef fishes and heterotrophic benthos groups, the schematic food web in Fig. 1 indicates an ecosystem composed of six trophic levels. To go from the estimate of net annual primary production of 2.73×10^6 kg/km^2 to the estimated annual production for the top predator of 462 kg/km^2 with six trophic levels requires a mean ecological efficiency of 17.6%.

Figure 1 reveals that only 19% of the reef fishes production and only 22% of the heterotrophic benthic production are consumed by predators outside these groups. This high proportion of internal predation is one reason fishery yields for the coral reef ecosystem are typically low relative to the high rate of primary production. It is also one reason there can be substantial variations in fishery yields due to the harvest strategy. For example, if harvests were limited to tunas, sharks, and jacks, the yield would not exceed 0.2 MT/km^2/year. However, if all the top predators are removed, a sustainable yield from the next lower level of about 6 MT/km^2/year which was going to the top predators can be harvested. Most of this yield comes from the reef habitat of 700 km^2 rather than the entire 1,200 km^2 habitat so the yield is actually about 11 MT/km^2/year. Although it is not known how much of this yield could actually be harvested with fishing gear, it is evident that, in theory at least, even this yield is not the MSY yield from this ecosystem since it could be exceeded if a harvesting strategy were employed to fish down the piscivorous reef fishes to reduce the internal predation in the reef fishes group. Sustainable yields have been reported for coral reef fisheries covering the range 0.1–18 MT/km^2/year (Marten and Polovina 1982).

Ecotrophic efficiency is defined by Ricker (1969) as the fraction of a prey species' annual production that is consumed by predators. A range of 0.66 to 0.75 is suggested as a range of the average ecotrophic efficiency in the marine ecosystems (Ricker 1969). Given our coral reef ecosystem which is estimated to consist of six trophic levels and an ecological efficiency of 0.17 and annual production at the top level of 462 kg/km^2/year, the level of net benthic primary production necessary to sustain the production at the top level can be estimated as a function of ectrophic efficiency (ee) as follows:

Net benthic primary production $= 462/[(0.17)(\text{ee})]^5$.

The net benthic primary production computed as a function of ecotrophic efficiency is given in Table 5. The net benthic primary production produced from the ECOPATH model of 4.3×10^6 kg/km^2/year corresponds to an ecosystem with an ecotrophic efficiency of 0.95 which suggests a very high level of predation mortality in the FFS ecosystem. If, for example, the ecotrophic efficiency for the ecosystem at FFS were only 0.5, then the net benthic primary production needed to drive the system would be 104×10^6 kg/km^2/year which is 25 times greater

Table 5. Net benthic primary production as a function of ecotrophic efficiency

Ecotrophic efficiency	Net benthic primary production ($\times 10^6$ kg/km^2/year)
1.00	3.3
0.95	4.2
0.90	5.5
0.85	7.3
0.80	9.9
0.75	13.7
0.70	19.4
0.65	28.0
0.60	41.8
0.55	64.7
0.50	104.1

than actual field measures (see Table 5 and Parts II and III of this paper).

Simple sensitivity analysis was performed on the input parameters (Polovina 1984). The estimate of mean annual biomass and total ecosystem biomass is relatively insensitive to changes in the energetics input parameters a and b, the nonpredation parameter d, and the apex B's. For example, on the average, an increase in a, the energetics parameter for growth, by 25% for a single species group only results in a 1.8% change in the average mean annual biomass for that species group and a 2.8% change in total biomass. However, the mean annual biomass is quite sensitive to changes in the *P/B* value. A 25% increase in the *P/B* value for a specific species group results in an average of almost a 22% change in the average mean annual biomass for that species group, and a 25% decrease in the *P/B* value for a specific species group results in an average of almost a 40% change in the average mean annual biomass for that species group. Fortunately, the sensitivity of the biomass estimate to changes in the *P/B* ratio is restricted only to the species group for which the parameter is being perturbed. The mean change in total ecosystem biomass is usually less than 8% for up to a 25% increase or decrease in the *P/B* parameter.

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AGING LONG-LIVED TROPICAL FISH USING DAILY GROWTH INCREMENTS[a)]

by

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Research has been underway for several years at the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service (NMFS) to improve upon existing methods of aging tropical fishes. Most people familiar with the subject are now aware that the otoliths of virtually all the fishes that have been studied to date grow by means of a daily episodic accretion of calcium carbonate. The episodic nature of the growth process leaves microscopic daily check marks which are commonly called "daily increments." The existence of daily increments in the otoliths of wide variety of marine and freshwater fishes has now been shown in temperate and tropical environments.

The occurence of daily increments in the otoliths of tropical fishes affords the opportunity of developing novel approaches to aging. Perhaps the simplest method used so far is to count all the increments present in an otolith, and to use the number obtained as an estimate of the age, in days, of the sample specimen. Although simple on theoretical grounds, there are a number of difficulties when attempts are made to age long-lived fish using daily growth increments.

I have devised a simple method which can overcome some of these difficulties. The method takes advantage of the fact that it is possible to measure the growth rate of the otolith by studying daily increments. A wide space between adjacent increments is interpreted to mean that the otolith grew rapidly in the intervening time interval. Conversely, a narrow space between adjacent increments indicated slow growth. The basic approach is to estimate the average width of daily increments at various points in the otolith. If the otolith were to grow at a constant rate, independent of the size of the fish, then increment widths would be uniform at all points in the otolith from focus to margin. If one could estimate this rate and the total length of the otolith, then the age of the specimen could simply be estimated by dividing the otolith length by its rate of growth.

Of course, otoliths do not grow at a constant rate and neither do whole fish. Nevertheless, this same process works well if one takes into account otolith and fish size. Usually, fish growth slows with age and approaches zero at an asymptotic size with increasing time. The same is true of otoliths. It is well known that the size of a fish is well correlated to the size of its otoliths.

In my method, the otolith is subdivided into regions which are small enough so that the growth of the otolith can be considered constant within subregions. I have found that within regions of about 500 microns the growth rate of the otolith is essentially uniform. The time it takes to grow through

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a) Abbreviated from "A novel approach to aging tropical fish", by the same author, ICLARM Newsletter, January 1985.

each one of these subregions is calculated exactly as outlined above. The average widths of daily increments within subregions (e.g., 0-500 microns, 500-1,000 microns, 1,000-1,500 microns, etc.) are determined by examining a number of preparations. Average increment width is then equated directly to the average growth rate of the otolith, measured in units of microns per day.

Typically, areas in which up to 25-30 increments are plainly visible are analyzed in detail. The total length of a short segment containing the increments is measured with an ocular micrometer and the total number of increments within the short segment is counted. The ratio of segment length to included increments provides an estimate of the average width of increments within the short segment. If one computes a number of such ratios, categorized by subregion, their mean values will provide an estimate of the average growth rate of the otolith in the subregion of interest. Once the relationship between otolith growth rate and otolith length has been determined, one calculates the length of time it takes to grow through each subregion by simple division. Next, the time intervals necessary for growth through each of the subregions are added together sequentially to estimate the total amount of time necessary for the otolith to reach a given size. It is then possible to convert otolith lengths to fish lengths with a regression equation of these variables. Ultimately one is left with a series of age at length determinations which can be fitted to any growth model desired.

The accompanying Table summarizes data obtained in this fashion for one of the many Hawaiian deepwater snappers, Pristipomoides auricilla. Note that, like the whole fish, the growth rate of the otolith declines as the size of the otolith increases. One can consider increment width (microns/increment) equal to otolith growth rate (microns/day) because there is a one to one correspondence between days and increments, at least as long as increments are deposited daily.

The data presented in the table were gathered after examining 220 short segments in 51 separate P. auricilla otolith preparations. These 220 segments contained an average of 14.25 daily increments each (s.d. = 5.6) so that a total of 3,135 increments were counted and measured in all. Furthermore, the average length of each short segment was 67.4 microns (s.d. = 43.8).

The results in the table summarize the method as applied to the available data. The amount of time necessary to grow through a length interval is simply the interval length divided by the average growth rate during the interval. Fish lengths were estimated from an independently derived regression on otolith length.

Summary of increment width and otolith growth rate analysis for *Pristipomoides auricilla.*

Otolith length interval (micron)	Mean otolith growth rate (micron/ day)	Time for interval growth (day)	Cumulative age through interval (day)	Length of fish-fork (cm)
0-500	29.04	17.22	17.22	3.4
500-1,000	20.05	24.94	42.16	6.4
1,000-1,500	18.88	26.48	68.64	9.3
1,500-2,000	7.99	62.56	131.20	12.1
2,000-2,500	5.55	90.04	221.24	14.9
2.500-3,000	4.92	101.57	322.81	17.6
3,000-3,500	3.92	127.42	450.23	20.3
3,500-4,000	3.41	146.74	596.97	23.0
4,000-4,500	2.28	219.35	816.32	25.6
5,000-5,500	1.64	303.95	1,401.88	30.9
5,500-6,000	1.53	326.53	1,728.41	33.4

It is apparent from the data that P. auricilla is relatively fast growing for members of this genus, reaching 50% of its maximum size of 42 cm in roughly 1.3 years. This fast growth is not surprising in light of its small adult size. Pristipomoides filamentosus, one of several larger species also under study, is known to exceed 80 cm, but does not reach 50% of its maximum size until well after three years of growth.

This simple method of aging tropical fish by estimating the widths of daily otolith increments is currently being evaluated at the Honolulu Laboratory. Results to date are encouraging.

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BIOLOGICAL CONSTRAINTS ON PRODUCTION AND RELATED MANAGEMENT ISSUES IN THE HAWAIIAN DEEPSEA HANDLINE FISHERY

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ABSTRACT

Specifically designed to gather data and information to meet the management needs of the Hawaiian deepsea handline fishery for demersal bottomfishes, a Sea Grant project (NI/R-7) was undertaken from 1976 to 1981. The resource in the main Hawaiian islands was assessed by surplus-production and yield-per-recruit methods to identify the extent of recruitment and/or growth-overfishing. The former analysis revealed that around the Maui-Lanai-Kahoolawe-Molokai (MLKM) bank, the main producer in the state, fishing activity is excessive relative to obtaining a maximum in sustained yield (MSY). The latter treatment demonstrated that at Penguin Bank an optimal level of fishing mortality is in effect for maximizing the growth potential of opakapaka, *Pristipomoides filamentosus*. These two assessments are consistent with the literature where it has been shown that MSY fishing mortality is generally restricted to values less than that which maximizes yield per recruit. In contrast with the main islands, the bottomfish resource of the Northwestern Hawaiian Islands is underutilized at present, where it is estimated that an annual harvest of at least 330 metric tons (MT) with an ex-vessel value of $2 million may be taken.

bottomfish
mortality
opakapaka
yield per recruit
surplus-production
maximum sustained yield

INTRODUCTION

The Hawaiian Archipelago stretches 1,500 nautical miles (nmi) from Cape Kumukahi on the island of Hawaii to Hancock

Seamounts, far to the northwest (Figure 1). The main high islands are basaltic formations and support all population centers in the state of Hawaii, but many small islands, pinnacles, and atolls extend for miles to the northwest, including Nihoa, Necker Island, French Frigate Shoals, Gardner Pinnacles, Laysan and Lisianski Islands, Pearl and Hermes Atoll, Midway Islands, and Kure Atoll. In addition to these largely uninhabited islands there are extensive shoal areas in the Northwestern Hawaiian Islands (NWHI) (e.g., Neva Shoal, Brooks Banks, St. Rogatien, Raita Bank, Maro Reef, and Hancock Seamounts).

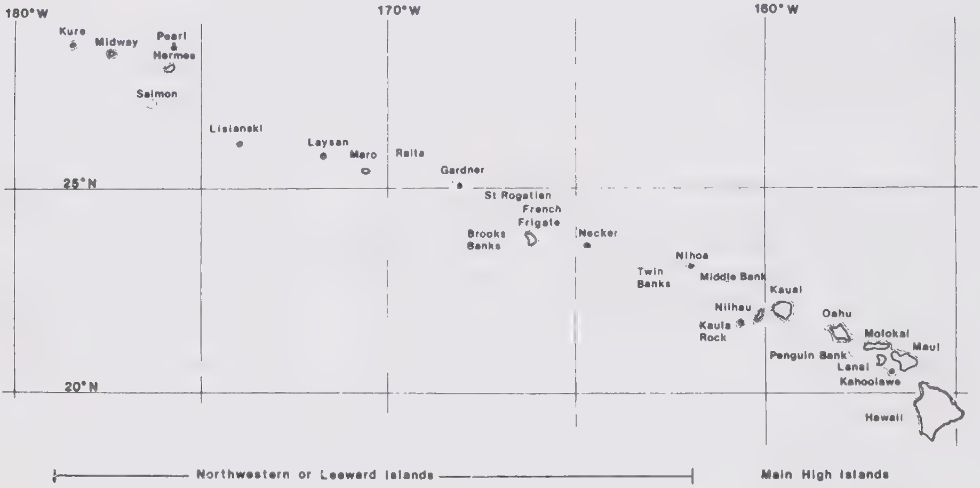
180°W
170°W
160°W
Kure
Midway
Pearl & Hermes
Salmon
Lisianski
Laysan
Maro
Raita
Gardner
25°N
St Rogatien
French Frigate
Brooks Banks
Necker
Nihoa
Twin Banks
Middle Bank
Kauai
Niihau
Kaula Rock
Oahu
Molokai
Maui
Penguin Bank
Lanai
Kahoolawe
Hawaii
20°N
Northwestern or Leeward Islands
Main High Islands

Figure 1. The Hawaiian Archipelago showing the approximate positions (dotted lines) of 100-fathom isobaths

Throughout the islands the myriad systems of submerged reefs, banks, and pinnacles harbor stocks or populations of commercially important bottomfishes. In particular, the snappers (Lutjanidae), groupers (Serranidae), and jacks (Carangidae) comprise some of the most valuable fishes harvested by the Hawaiian fishing industry, with some species at times commanding ex-vessel prices in excess of $15/kg. These are for the most part benthic fishes, in contrast with the pelagic tunas, living on or near the bottom in water depths of 20 to 200 fathoms. Most are found in regions of high physical relief which are thus unsuitable for trawling. They are caught almost exclusively with baited hook-and-line gear from fishing vessels which generally range in length from 7 to 30 m (Ralston, 1979). The mixed catch is marketed primarily in the round as fresh fish through several fish auctions and fishermen's cooperatives in the state.

In the past most fishing has been conducted around the main islands of the archipelago, especially at Penguin Bank off the island of Molokai (Figure 1) (Ralston and Polovina, 1982). However, as catch rates around the high Hawaiian islands declined and larger vessels entered the fishery, exploitation in the NWHI began to increase. Since 1976, when the extended 200-mile U.S. fishery conservation zone under the authority of the Magnuson Fishery Conservation and Management Act was implemented, interest in the bottomfish resources of the NWHI increased greatly. Recognizing these developments the Western Pacific Regional Fishery Management Council authorized the development of a fishery management plan for these stocks and emphasized the need to acquire biological information to manage the resource. At the time there had been no studies of these fishes in Hawaii and virtually nothing was known of their population dynamics (Ralston, 1979).

Accompanying this increased interest in the NWHI, the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, joined in a cooperative tripartite agreement in 1977 with the U.S. Fish and Wildlife Service (FWS) and the Hawaii Division of Aquatic Resources (DAR) to investigate the biotic resources of the area. Shortly thereafter the University of Hawaii Sea Grant College Program became a fourth active participant in the resource investigations of the NWHI. This Sea Grant project was initiated at that time with the intent of developing a basis for managing the deepsea handline fishery.

Since its inception, this project sought to gather data and information to meet the needs of fisheries management. This research project, "Development of a biological basis for managing the handline fishery for snapper and grouper population in the Hawaiian Archipelago", is now concluded and the proceedings of this second symposium on resource investigations in the NWHI offer an ideal forum for summarizing some of the project's more important findings. In this paper an overview is presented which specifically relates to management questions in the deepsea handline fishery. Almost all of the information presented here is a product of Sea Grant project NI/R-7, although relevant literature and outside data have been included where appropriate. However, most of the information resulting from this program has already been reported in a series of publications and manuscripts (Ralston, 1979, 1980a, 1980b, 1981a, 1981b, 1982; Ralston and Miyamoto, 1982, in press; Ralston and Polovina, 1982). Much of that which is presented here is summarized from this literature.

OBJECTIVES

From a management perspective the objective of the Sea Grant project was to assess the condition of bottomfish stocks in Hawaii relative to historical and present levels of exploitation. This fundamental problem was approached using two classical methods. In the first of these the entire bottomfish community was treated as a multispecies fishery and was analyzed by total biomass surplus-production methods. Twenty years of DAR catch statistics were summarized and Schaefer analyses performed at different levels of species aggregation (Ralston and Polovina, 1982). Results from this type of study are used to identity the latent capability of fish stocks to respond to exploitation in a compensatory fashion, and thus this first approach deals in a general sense with the question of recruitment/stock-overfishing. The second approach to stock assessment involved studying growth-overfishing in opakapaka, *Pristipomoides filamentosus*, the single most important species in the Hawaiian handline fishery. This problem was evaluated at steady state using of the Beverton and Holt (1957) yield-per-recruit year-class model in which opakapaka growth dynamics were determined by analyzing the width of daily otolith increments (Ralston and Miyamoto, 1982, in press) and mortality rates were estimated from catch curves after a regression model was formulated to permit development of an age-length key (Ralston, 1981b). In addition to the stock-production and dynamic-pool analyses (Beverton and Holt, 1957), ancillary studies of gear selection (Ralston, 1982), bottomfish depth distributions, and opakapaka reproductive biology provided other types of information which were useful not only from a biological/statistical perspective but from management's viewpoint as well.

SURPLUS-PRODUCTION ANALYSIS OF BOTTOMFISH

The basic premise of most stock-production models is that the per capita (i.e., weight specific) net productivity of a stock ($dB/B \cdot dt$) is a monotonic decreasing function of standing crop biomass (B). However, because total net production also depends in a positive way upon B, the greatest net production usually occurs at an intermediate level of standing crop. A maximum in sustained yield can then be obtained from a stock by cropping it annually to this specific level while harvesting the "latent" or "surplus" production. The fundamental problem then is to estimate this intermediate level and also the annual fishing effort needed to reach it.

The usual procedure is to assume that the catch rate or catch per unit of fishing effort (C/f) is in simple proportion to the biomass of standing crop and that fishing effort (f) is in simple proportion to fishing mortality. The empirically observed functional relationship between C/f and f can then be used to predict the response of the stock to exploitation. The well-known Graham-Schaefer model asserts that these two variables demonstrate an inverse linear relationship, from which it follows that the growth of the stock follows the logistic equation.

This seems to make good sense but there are serious deficiencies in this kind of approach. The most obvious is the inability of these models to adequately describe variation in stock age structure (but see Deriso, 1980). A ton of larvae, for example, responds differently to attempts at exploitation than does a ton of adults. Thus, to model a stock using biomass as the only stated variable is clearly an extreme simplification.

Another deficiency which is somewhat more subtle arises when determining the statistical relationship between C/f and f. An inverse association between these variables is expected even in the situation where catch and effort are completely independent-orthogonal random variables (Schnute, 1977; Mohn, 1980). Nevertheless, when these are the only statistics available, the use of surplus-production models can provide a crude but useful means of assessing the condition of a stock.

Accordingly, the status of the deepsea handline fishery in Hawaii was evaluated by application of the Graham-Schaefer model to 20 years of DAR catch statistics (Ralston and Polovina, 1982). Several problems unique to this specific fishery complicated this analysis. The first is the question of stock definition. At the present time there is insufficient information available to determine the extent of bottomfish larval dispersal between discrete islands of the archipelago. A recent starch-gel electrophoretic analysis of opakapaka enzyme systems failed to detect genetic differences from populations as widely separated as Molokai and Maro Reef, a distance of 750 nmi (Shaklee and Samollow unpublished manuscript). Negative biochemical evidence such as this is difficult to interpret, but does not disprove isolation although it does suggest intermixing of the stocks. Another problem, however, is that the total biomass model which was used in the analysis (Pope, 1979) pools catch statistics across different species, a procedure which contradicts all conventional notions of the unit stock.

A third problem was that an extensive history of fishing and corresponding catch statistics were available for high island areas only and were completely lacking for the NWHI. Consequently, this approach could only be used for the former region. Problems also arose in formulating a suitable measure of fishing effort and there were difficulties in dealing with the unreported recreational catch of bottomfish as well. Needless to say, a variety of assumptions were made but the analysis did provide internally consistent results which gave a reasonably clear indication of the status of bottomfish resources in the high Hawaiian islands.

The study demonstrated that the fishery could be effectively described by aggregating the catch statistics of the 13 major bottomfishes into 3 species groups identified by cluster analysis. No interactive effects were detected among these multispecies groups, as they seemed to behave as independent entities. Although there were strong correlations in fishing mortality among the groups, this was apparently due to fishing activity rather than having a biological basis.

Acceptable statistical results were only obtained from the Maui-Lanai-Kahoolawe-Molokai stock which alone accounted for over 50 percent of the total state landings of bottomfish. The maximum in sustained yield for this stock was estimated to be 106 metric tons per year, equivalent to 272 kg/nmi of 100-fathom isobath per year when standardized for habitat area. It was also determined that an annual fishing effort of about 900 fishermen (vessel)-days would result in a harvest equal to the projected MSY.

A plot of total annual landings of all bottomfish species reveals past trends as well as the current status of the MLKM fishery (Figure 2). It is apparent that from 1961 to 1963 an abrupt jump occurred in total landings (56 percent increase), leading to harvests moderately in excess of the estimate of MSY (18 percent above). In the 6 years after the peak harvests of 1963 and 1964 catches stabilized briefly around MSY but then a definite decline in bottomfish landings occurred which reached a nadir in 1970 at a level of 38 percent below MSY. Since that time catches of bottomfish increased for a while and as of 1980 the harvest hovered at a level somewhat less than MSY (10 percent below). At present there are no estimates available for the annual landings of 1981 or 1982.

This pattern of catches appears to be adequately explained by changing trends in fishing effort within the fishery (Figure 2). Rapid increases in effort during 1963 and 1964 were associated with the peak harvests of those years. These catches in excess of MSY may have been the results of disequilibrium and the "fishing up" effect (Ricker, 1975). The yield from the fishery then stabilized near MSY (1965-68) as fishing effort approached an optimal level. The reason for the abrupt decline in landings which occurred in 1970 is difficult to determine. The causality between the effects of catch on effort and, conversely, the effects of effort on catch are confounded in this instance. Although it is not certain whether the decline was due specifically to some kind of stock failure, there are at least two factors which support this possibility. The first is that fishing effort had been steadily increasing and was at a level in excess of optimal effort during 1968 and 1969, just prior to when landings fell. The second is that throughout the time period in question the ex-vessel price per pound of bottomfish was increasing. Figure 2 also shows that the average ex-vessel value of the catch rose from \$0.58/lb in 1963 to \$0.81/lb in 1970. These figures have been adjusted by consumer price indices for Honolulu and represent the actual deflated value of the catch measured in 1967 dollars. Thus, it is unlikely that the decline in landings could have been due to unfavorable market conditions for the product. Immediately following the decline of 1970, and perhaps as a result of it, fishing effort decreased to suboptimal levels in 1971 and 1972 and landings began to increase again. However, the level of fishing effort increased abruptly in 1973 and 1974 to levels substantially in excess of an optimal amount, and since that time yields have consistently been less than the Ralston and Polovina (1982) estimate of MSY. The obvious conclusion is that the fishery for bottomfish at the MLKM bank is now on the descending limb of the catch curve, with further increases in fishing effort likely to result in further decreases in catch. From the perspective of MSY the fishery appears to be overexploited.

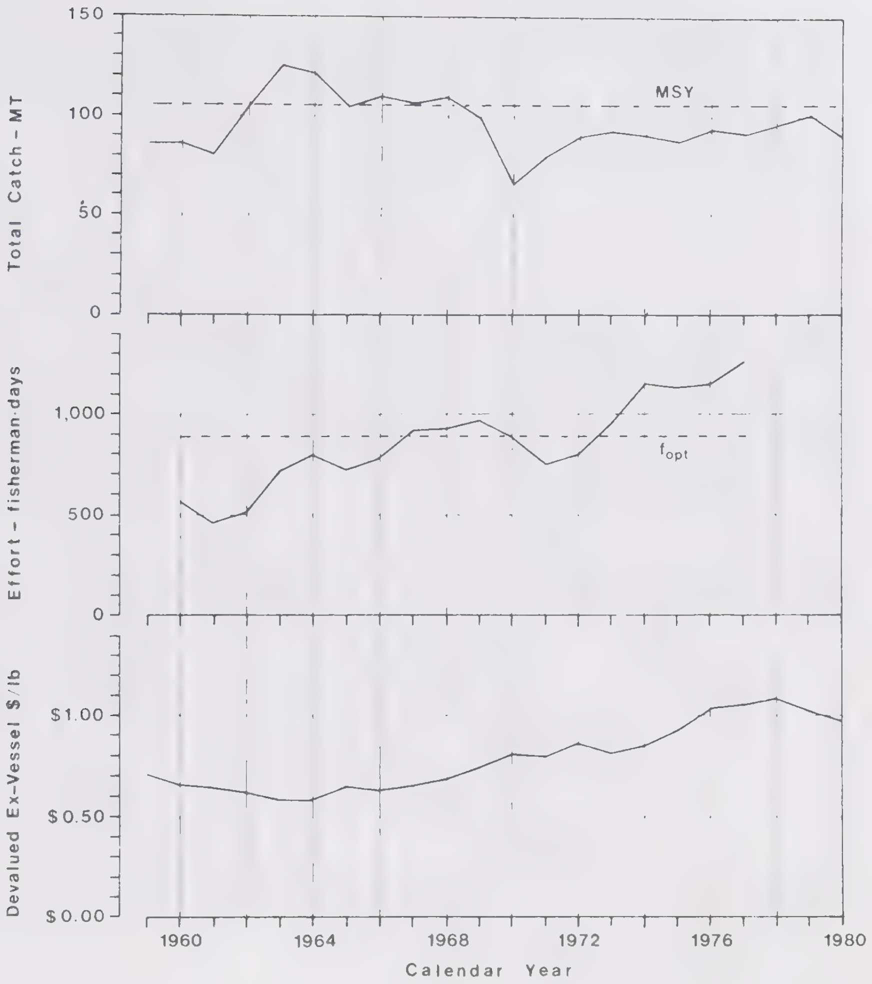

Figure 2. Trends (1959-80) within the fishery for bottomfish at the Maui-Lanai-Kahoolawe-Molokai bank. The top panel shows total catch relative to the estimate of maximum in sustanined yield, the middle panel shows annual fishing effort relative to the estimate of f_{opt}, and the bottom panel shows deflated ex-vessel price per pound in 1967 dollars.

Other aspects of the surplus-production study provide managers with food for thought if not concrete information on which to base policies. Two of these deserve mention here. The first relates to the estimate of MSY from the MLKM stock. Pope (1979) argued that if in a multispecies fishery exploitation is exerted in such a way that the fishing mortalities of the various species remain in constant ratio to one another, then use of the total biomass Schaefer model may have real meaning. However, he also showed that it cannot be concluded that an MSY estimated from the model need be the global maximum. These are relevant considerations because, as alluded to previously, there are high correlations of fishing effort among the three species groups. Thus, it is theoretically possible that a yield larger than 106 MT per year could be sustained if one could alter the ratios of fishing mortality among the species groups. This may not be an unrealistic proposition because the three groups are for the most part spatially separated. In principle, appropriate management action could thus reduce fishing on one group while simultaneously increasing that on another, but with the present state of our knowledge it would be futile to speculate about the possible extent of any increase in MSY resulting from such action.

A second outcome of the study worthy of consideration by managers involves the notion of species succession in multispecies fisheries. The production analysis of the three species groups comprising the MLKM stock suggested that each of the groups is characterized by its own unique combination of Malthusian parameter and carrying capacity. The trajectory of the system's biomass approaching a new equilibrium point would therefore be likely to undergo shifts in composition of one group relative to the others. In particular, the species group composed of ulua species (*Caranx* and *Carangoides* spp.); taape (*Lutjanus kasmira*); uku (*Aprion virescens*); and aawa (*Bodianus bilunulatus*) has a Malthusian parameter estimated to be almost twice that of the remaining two groups. If fishing were relaxed abruptly one would thus expect a transitory increase in the relative contribution of these species to the total harvest of bottomfish from the MLKM stock. Given that the economic value of the different species of bottomfish varies greatly, this may or may not be a desirable result of managing the resource.

YIELD PER RECRUIT ANALYSIS OF OPAKAPAKA

Consider the progression of a single year-class or cohort of fish through time. Early in its lifespan there are many very small recruits. Later on, due to the inevitable force of natural mortality, there are fewer fish alive but these are larger through growth. Only very few individuals ultimately survive to reach old age and large size. It is also true that at any point in time the cohort biomass is equal to the product of the number of individuals alive at the time and their average weight. Because within a year-class these two quantities are inversely related, that is to say, either many small fish are present or a few big ones, the biomass of a fish cohort usually reaches a maximum value at some intermediate stage in its lifespan. An optimum combination of size at harvest and probability of capture therefore exists which will maximize expected yield.

Beverton and Holt (1957) formalized these ideas and showed that the yield of a cohort over its fishable lifespan (t_c - t_λ)

equal to the integral of the product of instantaneous fishing mortality (F) and cohort biomass at time t. Yet, as noted previously, biomass is simply the product of the number of individuals alive times their average weight. Hence:

$$Y = \int_{t_c}^{t_\lambda} F \, . \, B(t) \, . \, dt = \int_{t_c}^{t_\lambda} F \, . \, N(t) \, . \, W(t) \, . \, dt$$

They also showed that under equilibrium conditions the yield of a cohort over its fishable lifespan is in effect equal to the annual yield from a fishery composed of mixed cohorts. Equilibrium conditions imply a relatively constant supply of recruits, constant fishing mortality over a time period equal to $t_\lambda - t_c$, and similar constancy in all the parameters which characterize the mortality N(t) and growth W(t) functions.

The solution to this equation provides a means of selecting optimal fishing mortality and age at entry to the fishery (t_c) so as to maintain high yields. If too much fishing mortality is inflicted early in life, a year-class will not have had sufficient opportunity for growth. Conversely, if harvesting is delayed too long, many individuals will be lost to natural mortality and with it their potential contribution to total yield.

This type of calculation addresses the question of growth-overfishing or harvesting fish before their optimal size is attained. The basic problem is to characterize the growth and mortality functions, W(t) and N(t), and this was attempted for opakapaka.

The growth of opakapaka was studied by examining daily growth increments which are known to be deposited in the otoliths of many fishes (Ralston and Miyamoto, 1982, in press). Because these growth marks are frequently difficult to resolve throughout an otolith, a method was devised to estimate the age of individual opakapaka, based upon the pattern of otolith growth rate as indicated by increment width. Integration of regression equations of otolith growth rate on otolith size provided estimates of specimen ages in days. The method proved to be reasonably accurate (the median coefficient of variation of age estimates was 6 percent) and was also successful in accounting for most of the variation in otolith growth rate (the median r^2 for all regressions was 77 percent) (Ralston and Miyamoto, 1982). One major finding was that growth in mature opakapaka seemed to be discontinuous, requiring restrictive assumptions about growth in this size range. Nevertheless, increment periodicity was validated by tetracycline injection of experimental fish and shifts in size-frequency modes of samples from French Frigate Shoals closely matched estimates of growth rate derived from the study of otoliths. Both estimates compared favorably with the available literature and a growth curve for opakapaka was ultimately obtained (Ralston and Miyamoto, in press).

Mortality rates were estimated from catch curves or age-frequency distributions. A regression approach to generating an age-length key for opakapaka was developed as a means of transforming length-frequency data into age-frequency distributions (Ralston, 1981b). In this procedure a nonlinear regression of age on length provided an equation for estimating mean age as a function of fish length. The squared deviations in age (i.e., residuals^2) from this fit were subsequently regressed on length as well, resulting in an equation for estimating the mean squared deviation in age (variance in age) as a function of length. These two equations provided estimates of mean age and variance in age as functions of length. An age-length probability matrix was then calculated using the normal distribution function which, when post-multiplied by a length-frequency column vector, resulted in another vector of estimated age frequencies (Ralston, 1981b).

This age-length probability matrix was applied to length-frequency samples of opakapaka from Penguin Bank, Necker Island, French Frigate Shoals, and Maro Reef (Figure 1). The resulting estimated age-frequency distributions were then analyzed by traditional catch curve methods and the total rate of instantaneous mortality (Z) and age at entry to the fishery were determined. Several estimates of Z were obtained from each locality, but ultimately a pooled mean estimate of total mortality rate ($\bar{Z}$), weighted by sample size, was calculated for each site under the assumption that populations were age-stationary. Figure 3 shows that $\bar{Z}$ is inversely related to distance to Honolulu. This is likely due to variation in fishing pressure along this gradient. At the time of the study, the stock at Maro Reef in the NWHI was for all practical purposes unfished. During the period 1959-78, only 31 catch records from this site were filed with DAR. For purposes of comparison, nearly 58,000 catch records were filed from Penguin Bank during the same period. Similarly, over 2,600 records were filed from Necker Island. If we assume that during the study fishing mortality (F) at Maro Reef was negligible, then the estimate of total mortality (0.22 per year) provides an estimate of natural mortality (M) because $Z = M + F$. This assumption seems to be reasonable because the calculated value of $\bar{Z}$ from Maro Reef is the lowest of all fishing banks examined. Natural mortality rate was predicted by the method suggested by Pauly (1980) as an independent check on this estimate, resulting in a predicted value of 0.32 per year. The agreement between the two estimates seems reasonable, and, as a representative figure for opakapaka natural mortality, a value of 0.25 per year was used in all subsequent analyses. Characterizing the rate of opakapaka natural mortality allowed separation of $\bar{Z}$ into its component parts. Thus, at Penguin Bank fishing mortality rate (F) was estimated to be 0.48 per year (0.73 minus 0.25).

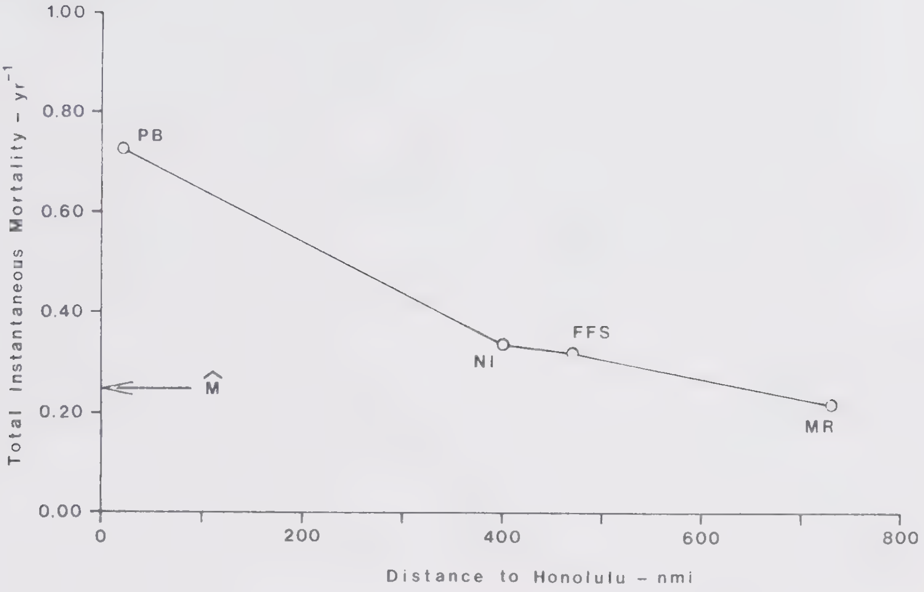

Figure 3. The relationship between the pooled mean total mortality rate ($\bar{Z}$) of opakapaka and distance to Honolulu. PB = Penguin Bank, NI = Necker Island, FFS = French Frigate Shoals, and MR = Maro Reef. The estimate of natural mortality is indicated by an arrow on the ordinate.

The foregoing results completed the determination of the opakapaka mortality function, N(t), which was then combined with the growth function, W(t), permitting numerical solution of the Beverton-Holt yield equation. The results are displayed graphically in Figure 4. In this figure constant values of yield per recruit (isopleths) are mapped onto a two-dimensional surface of management control (fishing mortality rate and age at entry to the fishery). Note that the eumetric fishing line is the locus of points which gives the maximum yield per recruit at fixed levels of fishing mortality. The single point on the isopleth surface represents Penguin Bank where $\hat{F}$ = 0.48 per year and $\hat{t}_c$ = 4.0 years.

From these results it is possible to conclude that there is little that could be done in the sense of growth-overfishing to improve the fishery for opakapaka at Penguin Bank. The specific combination of F and t_c at this site places it very close to the eumetric line. Estimated yield per recruit is about 0.36 kg per recruit and only very large increases in fishing mortality could increase this figure substantially. Such a policy would certainly risk recruitment-overfishing, violating a critical assumption of the model. From these considerations it is clear that the fishery for opakapaka at Penguin Bank is fortuitously close to an optimum level of exploitation inasmuch as the fishery has never been seriously regulated.

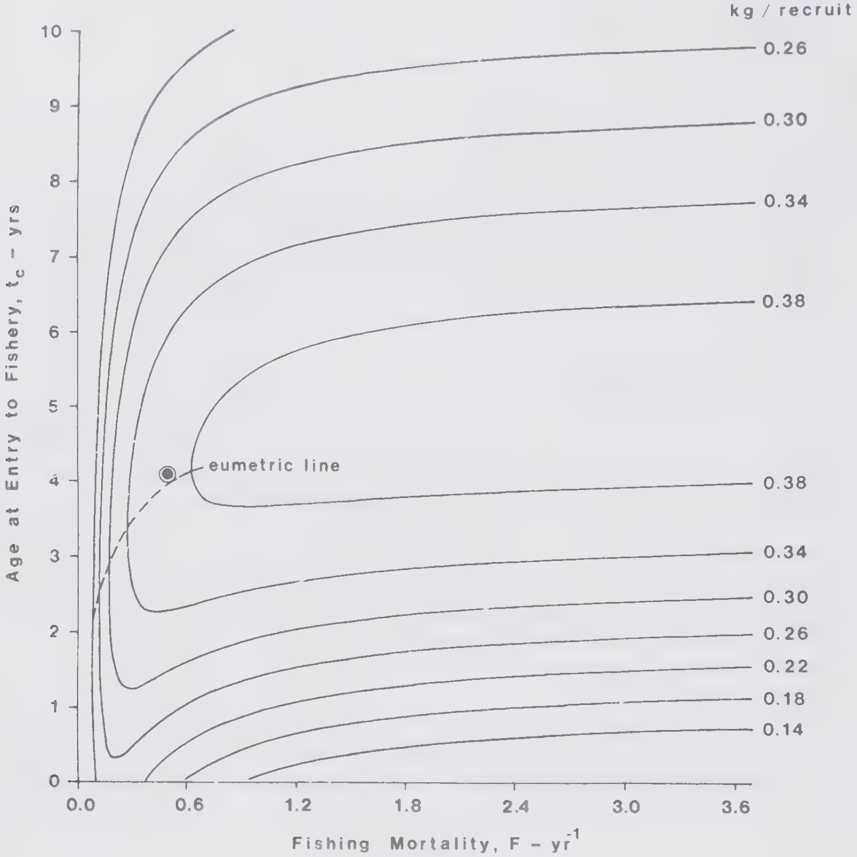

Figure 4. Beverton-Holt yield-per-recruit surface for opakapaka. The point represents the estimated position of Penguin Bank in 1980.

DISCUSSION

The results of both the surplus-production analysis of bottomfish from the MLKM stock and the yield-per-recruit analysis of opakapaka from Penguin Bank provide a coherent assessment of the present status of bottomfish populations. Landings from the fishery were estimated to be somewhat less than maximal in the former treatment, ostensibly as a result of overfishing. The latter study, on the other hand, suggested that in terms of optimizing the harvest of opakapaka growth potential few improvements were possible. On face value these two conclusions seem somewhat contradictory although a brief examination of the literature will show otherwise.

Recall from the yield-per-recruit analysis that the natural mortality rate of opakapaka at Maro Reef was estimated to be 0.25 per year whereas the total mortality rate of this species at Penguin Bank was determined to be 0.73 per year. If natural mortality at these two sites is comparable, and at the present time there is no reason to think otherwise, this implies a fishing mortality rate at Penguin Bank which is nearly twice as high as that due to natural causes. Other studies suggest this may be excessively high if yields are to be maximized by avoiding recruitment/stock-overfishing.

Alverson and Pereyra (1969), based on the unpublished ideas of Gulland (1971) and an earlier Soviet study (Tiurin, 1962), first proposed that at MSY the optimum level of fishing mortality (F_{opt}) was approximately equal to natural mortality. This particular conclusion applied not only to surplus-production models such as the Graham-Schaefer formulation, but more loosely to the Beverton-Holt constant recruitment model as well (Gulland, 1971). Saetersdal (1973) also advocated using M as a direct estimate of F_{opt} when assessing unexploited resources and when catch statistics are unavailable.

Francis (1974) examined more critically the theoretical basis of this approximation within the framework of the logistic growth equation. He concluded that the equivalence of mortality factors held only when recruitment was density-independent over a range in stock size spanning unexploited levels to one-half the virgin level (i.e., $R_o = R_{opt}$). More generally if the stock-recruitment relationship is best described by a Beverton-Holt type of spawner-recruit curve, or any other asymptotic form, then F_{opt} would likely be constrained to values less than M. Conversely, only when a Ricker or dome-shaped spawner-recruit relationship applies will F_{opt} likely exceed M.

Deriso (1982) expanded on these ideas and showed analytically two other factors of importance. The first and most significant of these is that MSY fishing mortality is often restricted to values less than the fishing mortality which maximizes yield per recruit. Thus, the relatively efficient utilization of opakapaka growth potential which characterizes the fishery at Penguin Bank is compatible with the notion of overexploitation from the perspective of MSY. The second point is that when a spawner-recruit curve is dome-shaped, F_{opt} can exceed M in the logistic model, but only in the situation where recruitment is severely depressed in the unexploited state (i.e., the stock displays strong recruitment compensation) will F_{opt} exceed 1.5(M). Other models such as Deriso's delay-difference formulation are more conservative in their behavior.

In view of the conclusions of these other studies it would seem that the analysis of the MLKM fishery presented here is internally consistent. Fishing there is excessive relative to obtaining MSY but is near optimal in terms of maximizing yield per recruit. A danger of recruitment-overfishing likely exists in this situation and yet it is fortuitous that with the historical lack of any serious constraints on fishing the stocks of bottomfishes have been as stable as they have, given the extent of exploitation at the MLKM bank. The situation is tenuous, however, and management of bottomfish resources around the main Hawaiian islands should certainly be considered now.

In contrast, the resources of the NWHI apparently have much potential yet to offer. Estimates of the total mortality rate of opakapaka from Necker Island and French Frigate Shoals (Figure 3) indicate that further increases in fishing activity should be easily assimilated by the stocks. Other fishing grounds remain totally untapped to the northwest of Maro Reef, where little fishing has occurred to date. While conflicts between fishing activity and the conservation of other wildlife resources (e.g., monk seals) remain unresolved, there nevertheless exists a bottomfish resource in the NWHI capable of supporting increased harvests on biological grounds.

As a first approximation to the magnitude of bottomfish resources in the NWHI, we can assume productivity comparable with the main high islands and invoke the Ralston and Polovina (1982) estimate of MSY per unit of habitat area (272 kg/nmi of 100-fathom isobath per year) for the MLKM stock. Because this figure does not include the recreational catch it provides a very conservative estimate of the potential yield of bottomfishes from the NWHI. These islands have a combined habitat area equivalent to about 1,200 nmi of 100-fathom isobath. Thus, one might expect as a minimum a sustained bottomfish yield of 330 MT per year from the NWHI. Given that the ex-vessel price per pound for these species is currently averaging about $2.75, the value of the resource to the fishermen might be estimated to be roughly $2 million annually. This amounts to a harvest substantially greater than that currently being landed in the main high islands of the archipelago.

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A New Species of Serranid Fish of the Genus *Anthias* from the Hawaiian Islands and Johnston Island[1]

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ABSTRACT: The serranid fish *Anthias fucinus* is described from 15 specimens collected from steep rocky slopes at depths of 168–198 m in the Hawaiian Islands and 214–237 m at Johnston Island. It is unique among the known species of the genus in lacking vomerine teeth. Other diagnostic characters are 9 soft anal rays (of the Indo-Pacific species of *Anthias* only *A. ventralis* has this count); 16 dorsal soft rays; 15 or 16 pectoral rays (all unbranched); lateral line with a distinct angle at anterior end of straight peduncular part, the pored scales 34–36 (only *A. boulengeri* from the Gulf of Oman has this number of pored scales); membranes of dorsal fin not incised; no prolonged dorsal spine (fourth or fifth spines barely longest); and a distinctive head color pattern of alternating stripes of violet and yellow.

THE FISHES OF THE GENUS *Anthias* (family Serranidae, subfamily Anthiinae) are small colorful species generally found on coral reefs or rocky bottoms in tropical and subtropical seas. They feed on zooplankton, usually in small aggregations a meter or more above the substratum, retiring to the shelter of the reef with the approach of danger. Because of their small size, they are not often caught by hook and line, and because of their association with hard irregular substrata, they are rarely captured in trawls. Most species live at depths greater than about 20 m. It was not until the advent of SCUBA that ichthyologists and aquarium fish collectors discovered the majority of the fishes of this genus that we know today. In a review of the literature of *Anthias*, Randall (1983) noted that 22 valid new species have been described from the Indo-Pacific region within the last decade. Anderson and Heemstra (1980) described two from the western Atlantic. Lubbock and Edwards (1981) named *Anthias salmopunctatus* as new from St. Paul's Rocks off Brazil. Still more remain on museum shelves to be named.

Randall (1979) reviewed the three Hawaiian species of *Anthias* known to him at that time, the endemic *A. thompsoni* (Fowler) and two widespread new species, *A. bicolor* and *A. ventralis*. The latter is subspecifically different in the Hawaiian region, hence was named *A. ventralis hawaiiensis*.

In November 1981 an unidentified 66-mm *Anthias* taken from the stomach of a large jack (*Caranx ignobilis*) collected by Farley Watanabe at St. Rogatien Bank in the Northwestern Hawaiian Islands was presented to the Bishop Museum. The jack was caught in 18 fathoms (33 m); the *Anthias*, however, was partially digested, thus could have been eaten at some other depth. Jacks of the genus *Caranx* are known to range individually over a broad range of depth; *C. ignobilis* has been observed off Hawaii by the senior author from a submarine at depths to 152 m. The head of the *Anthias*, much less digested than the body, was alternately striped with violet and yellow. Such a color pattern is not known for any other *Anthias*. Further examination confirmed the suspicion that this specimen represents an undescribed species; however, it was decided to wait for the collection of additional undamaged material for the description.

Dives in 1982 from the research submersible *Makali'i* by E. H. Chave, the authors, and others in the principal Hawaiian Islands

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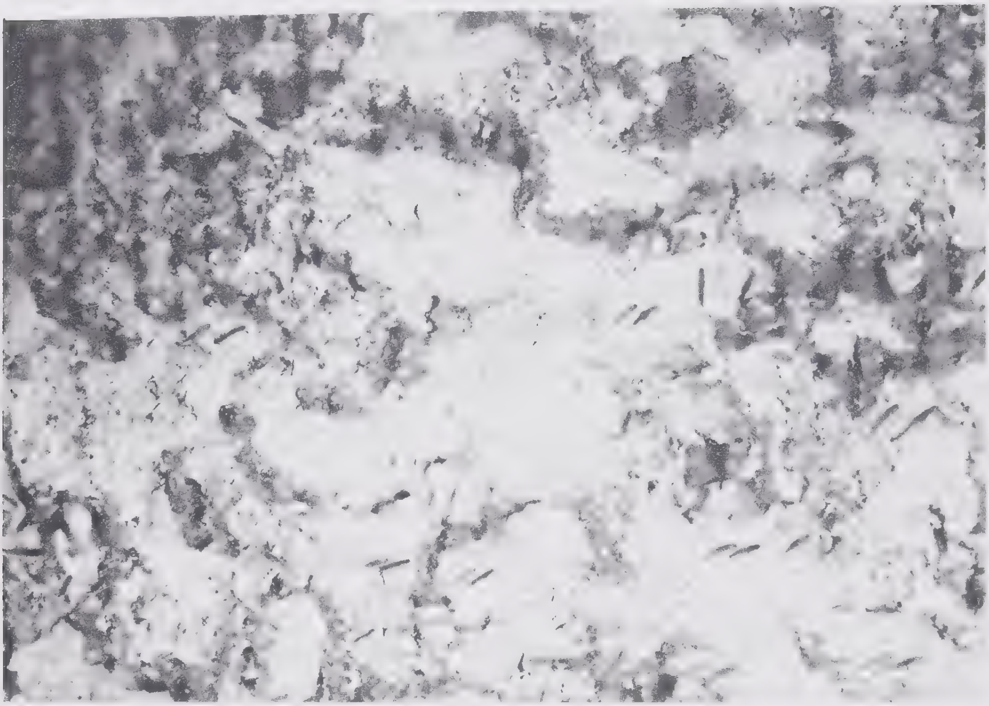

FIGURE 1. *Anthias fucinus* in 198 m off Johnston Island. Note that each fish has a well-defined shadow. Photograph from the submarine *Makali'i* by E. H. Chave.

revealed the abundant presence of this *Anthias* in the depth range of 135 to 210 m on steep, highly eroded slopes of ancient limestone. On 7 June 1982, Chave collected two specimens of the new *Anthias* in 198 m with rotenone from *Makali'i* at Penguin Bank off Molokai. The junior author collected four more from 168 m at the same locality on 15 September.

A year later a series of dives was made with *Makali'i* at Johnston Island by the authors, Chave, Phillip S. Lobel, and others. Again the *Anthias* proved to be abundant (Figure 1), this time in the depth range of 150–270 m. Lobel collected eight small specimens at the atoll from *Makali'i*.

The 15 specimens of the new *Anthias* are the basis for the present description. They have been deposited at the following museums: Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BM[NH]); California Academy of Sciences, San Francisco (CAS); National Science Museum, Tokyo (NSMT-P); Royal Ontario Museum, Toronto (ROM); J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa (RUSI); and National Museum of Natural History, Washington, D.C. (USNM).

The following definitions are given for the various measurements of fishes used in the present paper: standard length (SL) is the straight line distance from the front of the upper lip to the base of the caudal fin (posterior end of vertebral column); body depth is the maximum depth measured from the extreme base of the dorsal spines to the lowermost part of the abdomen (adjusting for any obvious malformation from preservation); body width is measured just posterior to the gill opening; head length is taken from the front of the upper lip in the median line to the posterior end of the opercular membrane; snout length is measured from the same anterior point to the fleshy edge of the orbit; orbit

TABLE 1

FIN RAY COUNTS OF HAWAIIAN SPECIES OF *Anthias*

SPECIES	DORSAL RAYS					ANAL SOFT RAYS				PECTORAL RAYS							
	X	XI	16	17	18	7	8	9	10	15	16	17	18	19	20	21	22
bicolor	26	2	1	21	6	26	2							10	17	1	
fucinus	15		15					15		7	8						
thompsoni	33		32	1		33									7	25	1
ventralis	19	1	1	17	2			19	1	19	1						

diameter is the greatest fleshy diameter of the orbit; interorbital width is the least bony width between the orbits; depth of caudal peduncle is the least depth; length of caudal peduncle is the horizontal distance from the rear base of the anal fin to the base of the caudal fin; fin spine and ray measurements are taken from their extreme bases (as seen from radiographs or from a bright light transmitted through the fish) to their distal ends; pectoral and pelvic fin lengths are the lengths of the longest rays; caudal concavity is the horizontal distance between verticals at the tips of the longest and shortest caudal rays.

Pectoral fin ray counts include the rudimentary upper ray; the last dorsal and anal fin rays are split to their base but counted as a single ray. Gill-raker counts include all rudiments; the raker at the angle is contained in the lower-limb count.

Data in parentheses in the descriptions below apply to paratypes. Proportional measurements are rounded to the nearest .05.

We provisionally place this new species in the genus *Anthias* pending a study of the generic classification of the Anthiinae. The need for such study has been expressed by Anderson and Heemstra (1980) and by Randall (1983).

Tables 1 to 3 provide a comparison of meristic data of the four Hawaiian species of *Anthias*.

Anthias fucinus, new species

Figures 1–4, Tables 1–4

HOLOTYPE: BPBM 28622, 54.6 mm SL, male, Hawaiian Islands, southwest end of Penguin Bank (20°52.4′ N, 157°39.3′ W), 170 m, rotenone from the research submersible *Makali'i*, S. Ralston, 15 September 1982.

PARATYPES: BPBM 28350, 66.0 mm SL (partially digested, with tail nearly severed), Northwest Hawaiian Islands, St. Rogatien Bank, from stomach of *Caranx ignobilis* caught in 33 m, F. Watanabe, 18 November 1981; BPBM 28123, 53.8 mm SL, same locality as holotype, 198 m, rotenone from *Makali'i*, E. H. Chave, 7 June 1982; BM(NH) 1983.12.22.3, 44.9 mm SL, same data as preceding; USNM 264611, 53.2 mm SL; RUSI 19798, 42.1 mm SL; AMS I.24334-001, 40.5 mm SL—all with same data as holotype; BPBM 29265, 3:22.7–24.0 mm, Johnston Island, outside reef at dump site (16 40.2′ N, 169°31′ W), 214 m, rotenone from *Makali'i*, P. S. Lobel, 13 September 1983; ROM 43016, 34.1 mm SL and CAS 54302, 27.9 mm SL, same data as preceding; BPBM 29267, 2:27.2–35.8 mm SL, Johnston Island, same locality as preceding, 237 m, P. S. Lobel, 14 September 1983; NSMT-P 22995, 33.0 mm SL, same data as preceding.

DIAGNOSIS: Dorsal rays X,16; anal rays III,9; pectoral rays 15–16, all unbranched; lateral-line scales 34–36; lateral line strongly arched anteriorly, only 1 1/2 scales separating it from middle and posterior dorsal spines, and forming an angle where straight peduncular part commences; no auxiliary scales; gill rakers 9–10 + 24–26; predorsal bones two; body depth 2.95–3.0 in SL; no papillae on posterior edge of orbit; front of upper lip of males not protuberant; no vomerine teeth; no prolonged dorsal spine (fourth or fifth spines longest, the remaining spines only slightly shorter); membranes of spinous portion of dorsal fin not incised; distal margin of soft

TABLE 2

LATERAL-LINE SCALE COUNTS OF HAWAIIAN SPECIES OF *Anthias*

SPECIES	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
bicolor																								2	5	4	6	6	2	2	1
fucinus	4	6	2																												
thompsoni																	1	1	2	6	8	7	4	2	2						
ventralis							2	2	6	6	1	2	1																		

TABLE 3

GILL-RAKER COUNTS OF HAWAIIAN SPECIES OF *Anthias**

	UPPER LIMB						LOWER LIMB						
SPECIES	7	8	9	10	11	12	22	23	24	25	26	27	28
bicolor					13	15					6	15	7
fucinus			5	7					6	5	1		
thompsoni				2	24	7				3	9	15	6
ventralis	1	14	5				4	7	6	3			

* Gill-raker counts were made on the first arch and include all rudiments; the raker at the angle is contained in the lower-limb count.

TABLE 4

PROPORTIONAL MEASUREMENTS OF TYPE SPECIMENS OF *Anthias fucinus* EXPRESSED AS A PERCENTAGE OF THE STANDARD LENGTH

	HOLOTYPE	PARATYPES						
	BPBM 28622	BPBM 29265	BPBM 29267	AMS I.24334-001	RUSI 19798	BM(NH) 1983.12/22/3	USNM 264611	BPBM 28123
Standard length (mm)	54.6	24.0	35.8	40.5	42.1	44.9	53.2	53.8
Body depth	33.5	33.1	31.5	31.9	33.3	34.1	32.8	31.4
Body width	15.6	16.7	16.5	15.1	15.9	16.9	16.9	15.4
Head length	33.0	36.6	34.8	34.8	33.7	33.9	34.7	33.0
Snout length	7.5	7.9	6.8	7.9	7.1	7.0	7.5	7.6
Orbit diameter	11.7	14.9	13.5	12.0	12.0	11.8	11.7	10.4
Interorbital width	7.3	7.7	7.7	7.7	7.1	7.2	7.3	7.1
Upper jaw length	16.5	16.5	16.8	16.0	16.5	16.2	15.8	15.1
Caudal peduncle depth	12.4	12.5	12.6	12.3	12.1	12.0	12.2	11.9
Caudal peduncle length	17.9	18.3	19.7	17.6	17.1	18.7	17.4	17.3
Predorsal length	31.7	34.4	33.2	34.6	33.7	33.0	32.6	32.7
Preanal length	60.0	61.2	60.1	61.0	61.3	60.1	61.0	62.1
Prepelvic length	33.2	33.2	34.1	33.6	33.0	32.1	33.4	33.1
Length of dorsal fin base	59.5	51.3	57.1	57.0	60.1	60.4	60.4	59.3
Length of first dorsal spine	7.3	8.4	7.8	7.9	8.5	7.8	7.2	7.4
Length of second dorsal spine	9.3	12.1	10.0	9.9	11.1	10.9	11.7	10.0
Length of longest dorsal spine	17.3	16.5	15.7	16.5	17.1	16.7	16.3	17.6
Length of tenth dorsal spine	16.1	14.7	14.7	15.8	16.6	15.6	15.4	17.6
Length of longest dorsal soft ray	22.5	20.8	20.9	19.2	19.5	21.6	20.7	20.9
Length of anal fin base	24.6	21.4	22.7	24.2	24.7	23.4	25.0	23.6
Length of first anal spine	6.6	8.1	7.0	7.2	7.4	7.8	6.8	6.6
Length of second anal spine	15.7	15.0	14.9	14.5	15.0	15.5	15.1	15.2
Length of third anal spine	17.7	15.4	15.2	14.5	16.5	15.6	16.6	16.3
Length of longest anal soft ray	26.2	21.2	21.5	20.2	20.0	20.9	24.8	24.2
Caudal fin length	47.5	broken	broken	broken	45.6	55.7	49.8	47.4
Caudal concavity	27.3	—	—	—	25.7	33.4	28.8	28.6
Pectoral fin length	35.6	35.9	33.7	36.8	36.1	39.0	36.0	36.4
Pelvic spine length	16.8	18.1	17.2	15.6	16.2	16.0	17.3	16.4
Pelvic fin length	43.6	30.0	36.1	36.8	41.1	37.2	40.3	37.9

portion of anal fin rounded; caudal fin lunate; pelvic fins long, 2.3–3.3 in SL; males with alternating stripes of violet and yellow on head; body yellow, suffused with orange-red on side below posterior part of dorsal fin, with irregular continuations of the violet stripes onto body, mainly broken into spots; females similar in color to males but dominantly yellow (the violet markings faint and the orange-red of the body largely absent).

DESCRIPTION: Dorsal rays X,16; anal rays III,9; pectoral rays 15 (15–16); pelvic rays I,5; principal caudal rays 15 (uppermost and lowermost unbranched); upper procurrent caudal rays 9; lower procurrent caudal rays 9; lateral line scales 35 (34–36); scales above lateral line to origin of dorsal fin $4\frac{1}{2}$; scales below lateral line to origin of anal fin 11; circumpeduncular scales 18; diagonal rows of scales on cheek between posterior edge of orbit and corner of preopercle 6; near-vertical rows of scales on opercle at level of middle opercular spine 4; gill rakers 10 + 24 (9–10 + 24–26); pseudobranchial filaments 12 (9–12, increasing with growth); branchiostegal rays seven; predorsal bones two, poorly developed (faint on radiographs), diagonal, the first anterior to first neural spine, the second pointing toward space between first and second neural spines (but not entering that space); vertebrae 10 + 16.

Body depth 3.0 (2.95–3.2) in SL; body width 2.15 (1.9–2.1) in depth; head length 3.0 (2.75–3.0) in SL; snout length 4.4 (4.35–5.1) in head; orbit diameter 2.8 (2.45–3.2) in head; interorbital space convex, the least width 4.5 (4.5–4.75) in head; least depth of caudal peduncle 2.65 (2.75–2.9) in head.

Mouth terminal, oblique (forming an angle of about 45° to the horizontal), the maxilla nearly reaching a vertical through rear edge of pupil, the upper jaw length 2.0 (2.05–2.2) in head; upper lip without an anterior fleshy protuberance (as seen in males of the subgenus *Mirolabrichthys*); upper jaw with a pair of small slender strongly recurved canine teeth anteriorly, separated by a gap at symphysis about equal to one-third orbit diameter (some paratypes with two close-set canines on each side); a row of slender canines along side of upper jaw posterior to anterior canines, these teeth progressively longer posteriorly, all but the first few curved anteriorly; an inner band of about three rows of small recurved teeth anteriorly in upper jaw, except for a large inner recumbent canine on each side of symphysis, the band soon narrowing to a single row along side of jaw; lower jaw with a pair of projecting medially curved canines anteriorly, a stout strongly recurved canine (or two such teeth) about one-fourth distance from front of jaw, and a single row of small slender canines along side of jaw, those toward the front curving posteriorly and those toward the rear curving anteriorly; three irregular rows of small incurved teeth behind anterior canines; vomer without detectable teeth; a few minute papillae on vomer and roof of mouth; palatines with about 15 very small teeth in two irregular rows. Tongue narrow and pointed, without distinct papillae. Gill rakers slender and long, the longest about half orbit diameter. Gill membranes free from isthmus.

Anterior nostril in a short membranous tube slightly above level of center of eye; posterior nostril a large irregular opening diagonally posterior and above the anterior; a very large pore directly in front of posterior nostril; a smaller but prominent pore in interorbital space above front of pupil of each eye; posterior half of orbit rimmed by a series of about 15 pores; no papillae along posterior edge of orbit; a series of five large pores along lower side of each mandible, and a pair of smaller pores at tip of chin.

Opercle with three flat spines, the largest and most posterior in the middle, closer to lower than upper spine; posterior margin of preopercle with 31 (12–35 serrae, the number increasing with growth) which are progressively larger ventrally; lower margin of preopercle and margins of subopercle and interopercle smooth.

Scales weakly ctenoid; no auxiliary scales; head scaled except lips, mandible, and snout (scales dorsally on head extending to level of posterior nostrils); no scales on dorsal and anal fins except for a row of small scales at extreme base (two rows anteriorly at base of anal fin); small scales extending more than half-way to posterior border of caudal fin and on about basal third of pectoral fins; pelvic axillary scale small (exposed part in holotype 0.7 mm); a triangular scaly process extending posteriorly from between bases of pelvic fins.

Lateral line complete, strongly arched anteriorly (only $1\frac{1}{2}$ scales separating it from middle and posterior dorsal spines) and forming a distinct angular part of one pored scale between curved dorsoanterior part and straight mid-lateral peduncular portion; last pored scale at end of hypural plate; tubules of lateral line simple and straight, covering nearly all of exposed part of scales.

Origin of dorsal fin slightly anterior to a vertical through upper end of gill opening; membranes of spinous portion of dorsal fin not incised; first dorsal spine about three-fourths length of second; fourth or fifth dorsal spines longest, 1.9 (1.85–2.2) in SL, the remaining spines nearly as long; sixth or seventh dorsal soft rays longest, 1.45 (1.55–1.8) in head; first dorsal soft ray unbranched, the remaining soft rays and all of the anal soft rays branched, the last to base; first anal spine about half length of second; second anal spine slightly stouter than third but slightly shorter; third anal spine 1.85 (2.0–2.4) in head; margin of anal fin rounded, the fifth or sixth rays longest, 1.25 (1.35–1.7) in head; caudal fin lunate, the lobes filamentous in adults, the caudal concavity 3.65 (3.0–5.0) in SL; pectoral fins moderately long, 2.8 (2.55–2.95) in SL, the rays unbranched; pelvic fins very long and filamentous (second soft ray longest), 2.3 (2.4–3.3) in SL.

Color of holotype in alcohol pale, the only dark pigment being a trace on anterior upper side, particularly along the front half of the lateral line where it forms a series of 17 small dusky spots. The paratypes lack dark pigment (though the 66-mm one from the jack stomach might have had this before it became a meal).

Color of holotype (a male) when fresh: head with alternating violet and yellow stripes, the uppermost violet band following dorsal contour of head, the second extending posteriorly from upper part of orbit, the third beginning at front of snout and passing through lower part of eye, the fourth extending posteriorly from maxilla; and the faint lowermost midventral on head; tip of lower jaw violet; body yellow, suffused with dull orange-red below posterior part of dorsal fin, with continuations of the violet stripes from the head, mainly as large irregular spots (the stripe from lower part of eye best developed, but very irregular with ventral extensions; see Figure 4); dorsal and anal fins lavender-blue with a violet margin (closer to pink on spinous portion of dorsal) and an irregular streak of dull yellow on most membranes paralleling rays; basal part of caudal fin yellow with violet markings, the outer part yellowish with lavender-blue markings, the upper and lower margins violet, the filaments yellowish; pectoral fins with clear membranes and pale pink rays; pelvic fins pale lavender-blue with a streak of yellowish on second to fifth rays, the filamentous ends of rays pink; iris with an inner ring of yellow and an outer of violet.

The color of the 53.8-mm female paratype (Figure 3) when fresh was basically the same as the male holotype but the violet stripes were poorly developed and the orange-red color on the upper side below the posterior part of the dorsal fin largely absent; there was more pale yellow and less blue on the dorsal, anal, and pelvic fins.

The color of the 35.8-mm subadult (Figure 2) was similar to the mature female, the most notable difference being an irregular streak of dull orange extending posteriorly from the orbit between the two lateral irregular pale violet bands of the head and body.

REMARKS

This lovely anthiine is named *fucinus* from the Latin for colored with orchil (a violet dye). It is at present known only from the Hawaiian Islands and Johnston Island.

In the Hawaiian Islands the species was common on the steep reef face of highly eroded limestone at depths of 135 to 210 m. The reef surface was pitted and cut with erosional channels about 3–40 cm deep which provided shelter for the fish. A fine layer of silt or sand covered the few near-horizontal surfaces. Except for occasional ahermatypic corals (yellow *Tubastrea*), the slope was nearly barren of sessile invertebrates. A species of galatheid crab, however, was abundant at the collection sites. Species of fishes associated with *Anthias fucinus* included *Holanthias fuscipinnis*, *Callanthias* sp., *Symphysanodon maunaloae*, *Suezichthys notatus*, and *Chaetodon modestus*. The most common larger predaceous fishes were *Seriola dumerili* and *Pristipomoides filamentosus*. The water temperature at the collection sites was 18°C.

At Johnston Atoll (16°44′ N) *Anthias fucinus* occurs in a comparable habitat but somewhat deeper, 150–270 m, with the peak abundance at 215 m. The temperature in this zone averaged 17°C. This suggests that sea temperature might control the depth distribution of the fish (i.e., to attain 17–18° water the fish must live at a greater depth at the atoll). One might expect the water off Johnston Island to be clearer than in the Hawaiian Islands, thus light would penetrate deeper and the level of illumination might be the major factor determining the depth at which this fish lives. However, measurements of water clarity at Penguin Bank (where the collections and most observations of *A. fucinus* were made) were essentially the same as those for the sea off Johnston (E. Chave, pers. comm.).

Anthias fucinus is not closely related to any known species of *Anthias*. It is unique in lacking vomerine teeth and in having all its pectoral rays unbranched as an adult. It is distinct from all species except *A. ventralis* (and less than 5 percent of the western Atlantic *A. tenuis* Nichols) in having nine soft anal rays. It has a lateral-line configuration similar to the Atlantic species of *Anthias* and *A. boulengeri* Heemstra from the Gulf of Oman (other Indo-Pacific *Anthias* have a smoothly curved lateral line without an angle at the start of the peduncular portion). The lateral-line scale count of *A. fucinus* (34–36) separates it from all Indo-Pacific species of the genus except *A. albofasciatus* Fowler and Bean. Only *A. boulengeri* has a lower lateral-line scale count (29–31). Both *A. albofasciatus* and *A. boulengeri* have 14 dorsal and 7 anal soft rays, hence are readily separated by these counts from *A. fucinus*.

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Assessing Gray Whale Abundance: A Review

Stephen B. Reilly

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Introduction

Recent estimates of gray whale abundance from two parts of the population's range are quite different in magnitude. Shore station censuses conducted during the north and south migrations range from about 15,000 to 20,000 for 1978 through 1980 (Chapters 10 and 13, this volume; Poole, 1984; Reilly *et al.*, 1983). The most recent estimate from an aerial census of the winter grounds is 7,600 for 1981 (Rice *et al.*, 1983). This is close to winter range estimates from the early 1970s (approximately 7,000 from Gard, 1974, 1978). The twofold disparity between estimates from different areas is an apparent dilemma. The two census types use different methods for data collection, different assumptions to infer total abundance, and have different problems.

This chapter reviews the history of gray whale population assessment and the methods and assumptions used by the two primary techniques. Estimating gray whale abundance is a difficult problem throughout their range. Each geographic–seasonal area presents specific difficulties, necessitating field and analytic techniques tailored to deal with differences in local abundance, distribution, habitat, and temporality of occupation. Neither assessment method is fully verified in its present state. (My personal bias favors the shore counts as being nearer to verification.) The winter range estimates

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are probably too low, but it is uncertain by how much. The shore station estimates are too high if gray whales in migration slow their rate of travel at night. There are reasonable scenarios under which the data from both locations can indicate similar population sizes.

In the following pages I first review the winter range assessments, then those from along the migratory route. Finally, I suggest how alterations in some of our assumptions for which little data exist can result in comparable population estimates from the data on hand.

Winter Range Assessment

On their winter grounds, gray whales occupy a vast area. The known range includes a number of physiographic settings within major and minor lagoons, near and offshore from lagoon entrances, and offshore zones throughout much of the west coast of the Baja Penninsula (Scammon, 1874; Gilmore, 1960; Rice *et al.*, 1981, 1983), parts of southern California (Chapter 14, this volume) and mainland Mexico (Gilmore *et al.*, 1967). Each subsection of each lagoon and alongshore area potentially requires individual and intense study for the design and execution of surveys of abundance.

Most winter range surveys have been made in small aircraft. Whales observed in the nearshore zone and within the lagoons were recorded (Gilmore, 1960; Hubbs and Hubbs, 1967; Gard, 1978; Rice *et al.*, 1981, 1983). The resulting raw data have consisted of counts per lagoon or per alongshore stretch. For abundance estimation, the problem is inferring total population size from these counts. This is essentially the same problem in any wildlife sighting survey, but the Baja situation presents some unique problems.

HISTORY AND METHODS

The history of population assessment on the winter grounds has been briefly outlined by Gard (1978), Rice *et al.* (1981), and Storro-Patterson (1981). Table I and the discussion which follows were drawn largely from those sources and from the original papers for some details.

There have been at least 21 separate aerial surveys of some portion of the winter range between 1952, when Carl and Laura Hubbs (1967) began the enterprise, and one in 1981 conducted by Rice *et al.* (1981, 1983) (Table I). Rice *et al.* (1981) stated that the winter range survey data are not comparable over time because of unstandardized field and analytic techniques, and I agree. The surveys were flown over varying portions of the winter range, along different track lines, at different times, and at different altitudes in varying visibility conditions, and so forth. Data treatment in analysis has been similarly nonstandardized.

This is not meant to depreciate past winter range aerial surveys. In the context of its time, each series contributed significantly to our knowledge. Our present understanding of the vastness of the area inhabited, and the complexity of the task of assessing abundance there, has emerged slowly. The logistic constraints (e.g., fuel limits, lack of

Table 1

Aerial Censuses of Gray Whales on the Winter Range

Dates	Observers	Areas surveyed[a]	Verification[b]	Source
1952 (Feb. 16–20)	Hubbs and Hubbs	1,2		Gilmore (1960)
1953 (Feb. 25–27)	Gilmore	1,2		Gilmore (1960)
1953 (Jan. 31–Feb. 4)	Rechnitzer	1,2		Gilmore (1960)
1954 (Feb. 14–21)	Hubbs and Hubbs	1,2		Gilmore (1960)
1954 (Feb. 1–7)	Gilmore	1,2,4		Gilmore (1960) Gilmore *et al.* (1967)
1955 (Feb. 26–Mar. 3)	Gilmore	1,2,4		Gilmore *et al.* (1967)
1956 (Feb. 14–17)	Gilmore	1,2,4		Gilmore *et al.* (1967)
1957 (Feb. 27–Mar. 3)	Gilmore	1,2,4		Gilmore *et al.* (1967)
1959 (Feb. 20–26)	Hubbs and Hubbs	1,2		Hubbs and Hubbs (1967)
1960 (Feb. 18–21)	Hubbs and Hubbs	1,2		Hubbs and Hubbs (1967)
1961 (Feb. 25–27)	Hubbs and Hubbs	1,2		Hubbs and Hubbs (1967)
1961 (Feb. 23)	Harrison	4		Gilmore *et al.* (1967)
1962 (Mar. 8–22)	Harrison	4		Gilmore *et al.* (1967)
1962 (Feb. 18–21)	Hubbs and Hubbs	1,2		Hubbs and Hubbs (1967)
1963 (Feb.–Mar. ?)	Harrison	4		Gilmore *et al.* (1967)
1964 (Feb. 20–24)	Hubbs and Hubbs	1,2		Hubbs and Hubbs (1967)
1965 (Jan. 3–Apr. 20)	Harrison	4		Gilmore *et al.* (1967)
1966 (Mar. 6–27)	Harrison	4		Gilmore *et al.* (1967)
1970 (Jan. 31–Feb. 1 and Mar. 4)	Gard	1		Gard (1974)
1973 (Feb. 27–28, Mar. 4)	Gard	1		Gard (1974)
1974 (Feb. 14–22)	Gard	1,2		Gard (1978)
1975 (Feb. 15–27)	Gard	1,2	1	Gard (1978)
1976 (Feb. 11–19)	Gard	1,2	2	Gard (1978)
1980 (Jan. 17–Mar. 28)	Swartz and Jones	5	3	Swartz and Jones (1980b)
1980 (Feb. 4–15)	Rice *et al.*	1,2	1,3	Rice *et al.* (1981)
1981 (Feb. 5–15)	Rice *et al.*	1,2,3	4	Rice *et al.* (1983)
1981 (Feb. 23–25)	Swartz and Jones	5	3	Swartz and Jones (1981)

[a] Areas: (1) nearshore Baja west coast, (2) calving lagoons, (3) offshore zones, (4) mainland calving areas, (5) Laguna San Ignacio only.

[b] Verification: (1) air versus lagoon tower, (2) ground-based behavioral observations for aerial correction factor, (3) air versus lagoon boat, (4) air versus offshore boat.

radio contact in case of emergency) imposed on anyone venturing to fly down Baja in a small plane in the 1950s and early 1960s effectively precluded offshore ventures and repetitious patterns over any one area (R. M. Gilmore, personal communication).

The early surveys conducted by Hubbs and Hubbs (during 1952, 1954, 1959, 1960, 1961, 1962, and 1964) and Gilmore (during 1953, 1954, 1955, 1956, and 1957) were pioneering efforts. However, the details of their efforts and methods are not made entirely clear in the published literature (e.g., Hubbs and Hubbs, 1967; Gilmore, 1960). They reportedly flew the entire coast from San Diego to the Cabo San Lucas area and over the major calving lagoons, tallying the whales seen. Hubbs and Hubbs (1967) discussed many potential sources of error and inconsistency in the methods used, including different aircraft, varying visibility conditions, dates surveyed, and number and experience of persons involved.

Gilmore (1960) gave a year-by-year summary of some further details of the early aerial censuses, enough to lend the reader a sense of the variation in methods used. Gilmore (1960, p. 29) also stated that early aerial surveys of the winter grounds were unreliable for estimating population size: "Because the air-survey method introduced many variable factors, and information needed to apply corrections was not available, it is unwise to estimate the size of the total population on air-survey data."

Although the early efforts conducted no ground-based verification experiments, it was acknowledged that many whales were not seen from the aircraft. Gilmore (1960) speculated that "About one-fourth of the whales beneath the plane could perhaps be seen by the observers at any one time." Hubbs and Hubbs (1967) assumed that "about half of the total population was observed in the area covered, and that almost all the individuals were concentrated in that area at the time of the counts . . ."

After a lapse of 5 years following the 1964 Hubbs survey, Gard (1974, 1978) conducted a series of six surveys in 1970 and in 1973 through 1976. In 1970 and 1973, only the major lagoons were surveyed; in later years coverage included the "entire western shore of Baja California." The distance offshore was not reported nor were full details on data-recording protocol. For the first time, separate censuses were made outside the entrances to the major lagoons to 3 km (1.8 mi) offshore. Gard's surveys were conducted during varying time periods in February and March. As with the earlier aerial surveys, track lines flown at each location, dates, and times of day were not reported. Consequently, it is not possible to determine to what extent his surveys were replicates of each other or of earlier attempts.

Gard was the first to address the problem of extrapolating from recorded counts to the total numbers present by directed data collecting during the winter ground surveys. He estimated the proportion of time gray whales spend at the surface, to determine what proportion might be missed by passing aircraft. Gard also compared his aerial estimates for Laguna Ojo de Liebre with ground-based counts made by White (1975). These verification experiments are discussed further in the section Assumptions and Summary (Winter Range).

In 1980 and 1981, Rice *et al.* (1981, 1983) conducted winter range aerial censuses, including the nearshore area between San Diego and Boca del Colorado (24° 20′N) and the known Baja calving areas. They also surveyed offshore areas in the large bays. To verify the overall surveys, tower, small boat, and aircraft studies were made in and near Laguna Ojo de Liebre in 1980. In 1981 they conducted a vessel survey of Vizcaino Bay during the same period as the aerial survey of that area. In both years replicate surveys were made of Lagunas Ojo de Liebre, Guerrero Negro, and San Ignacio. Dates, locations, and other details of survey segments were reported.

No estimate of population total was made by Rice *et al.* (1981) for the 1980 census, as the survey was considered exploratory for determination of total range and relative importance of areas within the range. A limitation of the 1980 (and 1981) surveys by Rice *et al.* is their southern termination at Boca del Colorado near Magdelena Bay. Both Norris *et al.* (1983) and Storro-Patterson (1981) report sighting congregations of gray whales in the Cabo Falso–Cabo San Lucas Region [174 were actually sighted by Norris *et al.* (1983)].

Rice *et al.* conducted the 1981 survey using three methodologies and related analysis schemes: "systematic transects" of open areas followed predefined straight parallel lines. Data were analysed as strip censuses for density estimates and variances; "coastline transects" were made along most of the outer coast covered. Only raw counts were used, and no extrapolations were made from these data; "channel transects" were made along narrow lagoon channels by flying along the channel sides so that its entire width was visible from one side of the plane. Again only raw counts were used for the population estimates, with no extrapolations for whales missed.

Total population estimates were made by Rice *et al.* (1983) for both adults and calves. For adults, statistical estimates from "systematic" transects were summed with raw counts from coastline and channel transects to produce an estimate of 7601.

Estimation of the number of calves was yet more complex, including ratio correction schemes for some areas and raw counts for others. The total estimate, summed from the combination of raw counts and various types of estimates, was 1439 calves. In relation to the estimate of 7601 "adults" by Rice *et al.* (1983), this indicates a crude birth rate near 19%. Other information, discussed below, suggests that either the "adult" estimate is too low or the calf estimate is too high, or both.

ASSUMPTIONS AND SUMMARY OF CURRENT STATUS

A list of factors affecting or involved in estimating total abundance from winter range aerial surveys is presented in Appendix A. This list is admittedly armchair in nature (and in extent), but I believe that all of the points mentioned require at least minimal attention before we can have a great deal of confidence in population estimates from the winter range. Fortunately, many of these points have been or are being addressed by past or present research. A quantitative synthesis of the winter range assessment situation is the most outstanding current need. Some of the verification work done to date is discussed in the following sections.

Behavior

A considerable amount of information on behavior has been accumulated by ground-based research projects in the calving lagoons: in Laguna San Ignacio (LSI) by

Swartz and Jones (1978, 1980a,b, 1981, this volume); in Laguna Guerrero Negro (LGN) by Bryant *et al.* (this volume); in Laguna Ojo de Liebre (LOL) by Rice *et al.* (1981, 1983), Fleischer (1984), and White (1975); and by Norris *et al.* (1977, 1983) in and near Magdelena Bay.

In conjunction with his overall surveys, Gard (1978) timed the above- and below-surface occurrence for 25 groups of whales for a minimum of 3 min each, in and outside of LSI and LOL. Pooling the data by location and type of social group (cow–calf versus others), Gard estimated that gray whales on average spent 29.7% of their time at the surface. Consequently he multiplied observed aerial counts by a factor of 1/0.297 or 3.37.

Recent attempts by S. L. Swartz and M. L. Jones (personal communication) to replicate this study in LSI met with severe logistic problems. They found it extremely difficult to identify and follow individuals or groups for periods sufficiently long to record meaningful data. According to Swartz and Jones, a wide variety of types of behavior can be noted from any one vantage point, ranging from rapid traveling to quiescent lolling. They found surface times in general to be markedly variable in the lagoons. Consequently, the use of the mean surface time as a correction factor without considering its variance is questionable.

Much less detailed observation has been made outside the lagoons, where Rice *et al.* (1981, 1983) recorded nearly 70% of the whales observed in their survey during the peak occurrence period in February. Rice *et al.* (1983) performed a ship-based strip transect survey in Vizcaino Bay (see below), and Norris *et al.* (1983) recorded occurrences and some behavioral observations at the entrance to the Magdalena Bay complex. We now need additional detailed, systematic observations on behavior outside the lagoons in open coast and other areas of whale concentration which emphasize age, sex, temporal, and physiographic differences in activity. These data are necessary to determine if whales in along shore regions are differentially "available" to our observation from passing survey aircraft, and how much variability should be expected from replicate flights over each area.

Geographic Distribution

As recent surveys have expanded their efforts, new, and in some cases large, concentrations of whales have been seen in previously under- or unsurveyed areas: Vizcaino Bay is one example. Even the latest surveys probably did not cover the entire winter range.

It is apparently appropriate to consider the winter range as extending from about Point Conception in the north to Cabo San Lucas, including the Gulf of California and parts of the Mexican mainland (Chapter 14, this volume). In February when the Baja occupation is at its peak, there are still a few individuals passing Monterey (California) both north and southbound. There is probably no one time when the entire population is between San Diego and Magdalena Bay, the termination points of the latest surveys. There has been considerable coverage of smaller scale distribution in and near the major calving areas.

Interplatform Comparisons

Aerial to ground comparisons have been made for LOL and Vizcaino Bay (Gard, 1978; Rice *et al.*, 1981, 1983), and LSI (Swartz and Jones, 1981). Gard (1978) first compared counts obtained from the air and on the ground, for LOL. For a comparison period in mid-February 1975, he estimated 2013 adult whales inhabited LOL. For approximately the same period, White (1975) estimated 1963 as the adult population within LOL. This is compared to a February 1980 estimate of 895 for LOL by Rice *et al.* (1981).

That the aerial and land estimates were within 3% suggests either that both Gard (1978) and White (1975) had developed accurate assessment procedures or that the procedures perhaps were similarly biased. Even with the benefit of hindsight, it is not yet possible to distinguish between these possibilities, but some points regarding their methods are worth considering.

First, White's (1975) method consisted of monitoring the lagoon entrance from a tower for varying periods per day and week, subtracting weekly average exits per hour from average entrances per hour and multiplying the difference by 168 hr/week. Recent, similar observations of all daylight hours for 7 days per week (Rice *et al.*, 1981) have shown a great deal of variation in turnover rates. This and other lagoon studies (Swartz and Jones, 1978, 1980a,b, 1981; Norris *et al.*, 1977, 1983) suggested that turnover rates are probably more reflective of tidal fluxes and visibility conditions than actual abundance of whales in the lagoons. Second, Gard's (1978) aerial data also showed a great deal of variation between replicate surveys of the same areas. Third, as discussed above there is some question regarding estimation of the surface time statistic and its use as a correction factor.

In the lagoon comparisons, small single-engined aircraft were the principal platform. Because of this, results may not be equally applicable to the larger twin-engined aircraft (which were used for the comprehensive surveys) due to possible differences in visual perspective from the two types of planes. If air speed and altitude are not duplicated, this would exacerbate any such lack of comparability.

Visibility Conditions

Rice *et al.* (1983) found that weather and visibility conditions had a major effect on sighting efficiency in their repeated vessel and aerial censuses of Vizcaino Bay. Their results implied that other censuses made in less than adequate visibility conditions, such as nearly every afternoon on the Baja west coast when the strong prevailing wind blows, are probably negatively biased. I am aware of no other winter range data which represent visibility effects on census results.

In summary, the recent surveys have made notable progress toward an effective, standardized field methodology for estimating gray whale abundance on the winter range. We now need (1) a survey effort that covers the entire range and somewhat beyond to effectively define its limits. Further refinement of area- and time-specific field methods would also contribute to a reliable data base. (2) A more rigorous analytic methodology is also needed. All counts from an airplane are in fact estimates, with inherent variance. The basic properties, at least, of each type of estimate must be defined before they can be combined to give crudely comprehensive estimates of total and variance.

There are many nontrivial problems involved in the development of a more rigorous analytic methodology for the Baja survey situation, and much difficult work remains. Some important points which have emerged from winter range surveys to date are (1) aircraft are necessary to cover the entire area in a short time, but censuses from them systematically underestimate whale presence; and (2) interreplicate variation is high and is greatly affected by visibility conditions.

Migratory Route Assessment

Gray whales travel very close to shore, especially during their southward trek from feeding to calving grounds (Pike, 1962; Rice and Wolman, 1971). It is consequently feasible to census, from strategic points, whales passing during daylight hours. As with winter range aerial surveys, the essence of the resulting estimation problem is inferring total population size from recorded counts. There are still a number of problems to confront when inferring population size from these data, but the magnitude and scope of these problems is considerably smaller and more tractable than those resulting from winter range aerial surveys. The relative simplicity results largely from having only one site's complexities to deal with and not having to rely on instantaneous glimpses from airplanes for measuring absolute abundance. Also, the vast majority of the population is likely to pass a location that is well chosen.

HISTORY AND METHODS

An outline summary of in-migration censuses is presented in Table II. Townsend (1887) reported the first shore census of migrating gray whales from a sighting effort that was limited to December, 1885. Townsend identified three of the basic problems common to all shore counts made to estimate total abundance: How many whales pass unseen at night? on days before and after the census? too far offshore to be seen? Regarding his observed total, Townsend stated "What proportion this number bears to the number passing offshore would be hard to say, but it is certainly less than half. . . ."

Carl Hubbs, of the Scripps Institution of Oceanography in La Jolla, organized the next attempts at censusing southbound migrating gray whales 61 years later, in 1946–1947 (Walker, 1949). These counts, made by students from a campus rooftop, were continued through 1951–1952 (skipping 1950–1951). The details of effort expended are not clear in the published accounts (Walker, 1949; Gilmore 1960). The recorded annual counts were 250, 500, 600, 600, and 880, respectively.

During 1952–1953, the U.S. Fish and Wildlife Service conducted censuses of southbound migrating gray whales from San Diego, supervised by Dr. Raymond Gilmore (1960). Point Loma was the principal census site, although some concurrent censusing was done at La Jolla. These early San Diego censuses are of questionable utility as measures of population abundance for a number of reasons. By the mid-1960s, it became clear that a large (but as yet undefined) proportion of southward migrating whales passed far offshore through the Southern California Bight (Rice, 1965). This

Table II
Shore Station Censuses of Gray Whales

Dates	Migration direction	Observers	Location	Source
1885–1886 (December)	S	C. H. Townsend	San Simeon, California	Townsend (1887)
1946–1947 (Dec.–Jan.?)	S	Hubbs and students	La Jolla, California	Gilmore (1960); Walker (1949)
1947–1948 (Dec.–Jan.?)	S	Hubbs and students	La Jolla, California	Gilmore (1960); Walker (1949)
1948–1949 (Dec.–Jan.?)	S	Hubbs and students	La Jolla, California	Gilmore (1960); Walker (1949)
1949–1950 (Dec.–Jan.?)	S	Hubbs and students	La Jolla, California	Gilmore (1960); Walker (1949)
1951–1952 (Dec.–Jan.?)	S	Hubbs and students	La Jolla, California	Gilmore (1960); Walker (1949)
1952–1953 (Dec. 15–Feb. 15)	S	Gilmore	Pt. Loma and La Jolla	Gilmore (1960)
1953–1954 (Dec. 15–Feb. 15)	S	Gilmore	Pt. Loma and La Jolla	Gilmore (1960)
1954–1955 (Dec. 15–Feb. 15)	S	Gilmore	La Jolla	Gilmore (1960)
1955–1956 (Dec. 15–Feb. 15)	S	Gilmore	La Jolla	Gilmore (1960)
1956–1957 (Nov. 2–Mar. 25)	S	Gilmore	La Jolla	Gilmore (1960)
1959–1960 (Dec. 14–Feb. 22)	S	Gilmore	La Jolla	Rice (1961)
1966–1967 (Nov. 27–Feb. 17)	S	Adams	Point Lobos, California	Adams (1968)
1967–1968 (Dec. 18–Feb. 3)	S	Rice and Wolman	Yankee Point, California	Reilly *et al.* (1983)
1967–1968 (Dec. 18–Feb. 5)	S	Rice and Wolman	Point Loma	D. W. Rice and A. A. Wolman (unpublished)
1968–1969 (Dec. 10–Feb. 6)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1968–1969 (Dec. 20–Feb. 14)	S	Rice and Wolman	Point Loma	D. W. Rice and A. A. Wolman (unpublished)
1969–1970 (Dec. 8–Feb. 8)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1970–1971 (Dec. 9–Feb. 12)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1971–1972 (Dec. 18–Feb. 7)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1972–1973 (Dec. 16–Feb. 16)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1973–1974 (Dec. 14–Feb. 8)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1974–1975 (Dec. 10–Feb. 7)	S	Rice and Wolman	Yankee Point	Reilly *et al.* (1983)
1975–1976 (Dec. 10–Feb. 3)	S	Rice and Wolman	Granite Canyon, California	Reilly *et al.* (1983)
1975–1976 (Dec. 15–Feb. 11)	S	Rice and Wolman	Point Loma	D. W. Rice and A. A. Wolman (unpublished)

(*continued*)

Table II (*Continued*)

Dates	Migration direction	Observers	Location	Source
1976–1977 (Dec. 10–Feb. 6)	S	Rice and Wolman	Granite Canyon	Reilly *et al.* (1983)
1976–1977 (Dec. 15–Feb.?)	S	Rice and Wolman	Point Loma	D. W. Rice and A. A. Wolman (unpublished)
1977 (?)	N	Hall *et al.*	Unimak Pass, Alaska	Hall *et al.* (1977)
1977 (Nov. 20–Dec. 9)	S	Rugh	Unimak Pass. Alaska	Rugh and Braham (1979)
1977–1978 (Dec. 15–Feb.)	S	Rice and Wolman	Point Loma	D. W. Rice and A. A. Wolman (unpublished)
1978 (Nov. 7–Dec. 20)	S	Rugh	Unimak Pass	Rugh (Chapter 10, this volume)
1978–1979 (Dec. 2–Feb. 1)	S	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 12, this volume)
1978–1979 (Dec. 10–Feb. 8)	S	Rice and Wolman	Granite Canyon	Reilly *et al.* (1983)
1979–1980 (Oct. 31–Jan. 3)	S	Rugh	Unimak Pass	Rugh (Chapter 10, this volume)
1979 (Feb. 27–?)	N	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 13, this volume)
1979–1980 (Dec. 11–Feb. 4)	S	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 13, this volume)
1979–1980 (Dec. 10–Feb. 6)	S	Rice and Wolman	Granite Canyon	Reilly *et al.* (1983)
1980 (Feb. 21–?)	N	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 13, this volume)
1980 (Mar. 10–May 31)	N	Poole	Piedras Blancas	Poole (Chapter 16,this volume)
1980–1981 (Dec. 10–Feb. 9)	S	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 13, this volume)
1981 (Feb. 22–?)	N	Herzing and Mate	Newport, Oregon	Herzing and Mate (Chapter 13, this volume)
1981 (Feb. 9–May 30)	N	Poole	Piedras Blancas	Poole (Chapter 16, this volume)
1981 (Mar. 23–Jun. 17)	N	Hessing	Unimak Pass	Hessing (1983)

proportion may have changed throughout the years, in response to increasing levels of boating and other human activities nearshore (Gilmore, 1978a). The method used to correct for whales missed due to poor visibility was rather arbitrary for the first 3 years, being based on a subjective appraisal of the percentage reduction in visibility each day. Effort expended varied between years. For these and other reasons (discussed in Reilly,

1984) it is inadvisable to look to the early Point Loma censuses for accurate measures of abundance. However, through trial and error these early shore censuses did establish much of the basic field methodology that was used by subsequent censuses through the 1979–1980 Monterey study.

Five more censuses were conducted at Point Loma between 1967–1968 and 1977–1978. Although field and data recording procedures were well systemized in those years, including detailed observations on visibility conditions, these data are also of questionable accuracy because of the unknown proportion passing offshore.

In 1966–1967, Adams (1968) conducted a fall census from Point Lobos, near Monterey, California. Rather than censusing all day during each day of the migration, he counted only during periods of good visibility and when convenient (his was a privately conducted and funded venture). The period of November 27 through February 17 reported includes the full duration of the southern migration near Monterey (Reilly *et al.*, 1980). Actual effort expended and raw counts are not reported. From average counts during hours watched, Adams extrapolated over the remainder of the day. The method sounds reasonable, but the results are questionable. A histogram (his Fig. 1) shows a maximum of about 55 whales per hour counted, with a number of days above 40/hr on average. This is almost certainly too high. In the highest days during the 13-year NMFS Monterey series, the average observed daily count was never more than 25 whales/hr. In no single hour did more than 30 whales pass the station (Reilly, 1981). Using arbitrary extrapolations of 70% daylight count for whales passing at night and 5% for whales passing offshore, Adams estimated the total population in 1966–1967 to be 18,300. As with the average hourly count, this is probably too high. The upper 95% confidence limit for the 1967–1968 census from Monterey was only 15,597 (Reilly *et al.*, 1983). This comparison assumes that the Monterey census was unbiased.

In 1967–1968, Dale Rice and Allen Wolman of the Marine Mammal Laboratory (Seattle) began a 13-year series of consecutive annual censuses near Monterey, California. These censuses were made from Yankee Point until 1973–1974, and from Granite Canyon (3.7 km south of Yankee Point) in the remaining years. Boat traffic is at a minimum in the vicinity of these sites along the beginning of the "Big Sur" coast. Further, there are no nearshore islands which might divert some whales offshore, as suggested for the southern California Bight south of Point Conception (Rice, 1965; Gilmore, 1978b).

At Monterey, counts were conducted for 10 hours per day (the duration of daylight) during approximately 2 months each year. Estimates were recorded of the number of whales present in each passing group and the distances of the groups offshore. Details of visibility conditions were also recorded. Areas considered in abundance estimation included the effects of varying visibility conditions, observer accuracy in estimating the number within and distance to passing pods, whales missed as a function of their distance offshore, those passing at night, and those passing before the first and after the last days of censusing. Raw counts recorded during 10 daylight hours ranged from a low of 2,667 in 1971–1972 to a high of 4,924 in 1979–1980. For this final year the "best estimate" of total abundance was 15,647, with 95% confidence limits of 13,450 and 19,201. (Confidence limits refer to precision here and assume an unbiased estimate.)

In November and December of 1977, 1978, and 1979, David Rugh conducted censuses from Cape Sarichef in Unimak Pass, Alaska (Rugh and Braham, 1979; Chapter 10, this volume). This is the point at which the population filters into and out of the Bering Sea. The first season comprised only 20 days during which 2,055 whales were observed in 82.6 hr of systematic watch. During 1978 and 1979, the duration of the census was extended in an attempt to cover the entire migration. Mean counts recorded those years were 5,050 and 4,061. Rugh also conducted experiments to verify some of the assumptions necessary to extrapolate to total population size. As with the California censuses, the most important estimation problem regarded the number of whales passing at night (approximately 16 of 24 hr at Unimak Pass are in darkness during November and December). Other areas considered but not applied to the abundance estimation included the "tails" of the migration, whales missed due to varying visibility and storm conditions, offshore distribution, differences among observers, and accuracy in counts even in ideal conditions. A "best estimate" was given for 1978 only of approximately 17,000.

The first attempt to census northbound gray whales during their spring migration was made by Hall *et al.* (1977) at Unimak Pass in 1976. The duration of the spring migration, nearly 4 months, makes it more difficult to census than the 2-month (or less) fall migration. The duration of the Hall *et al.* census was less than 2 months, and they estimated that only 9000 whales passed into the Bering Sea during the census.

During 1978, 1979, and 1980, counts were conducted by Herzing and Mate (Chapter 13, this volume) (of Oregon State University) from Yaquina Head in Newport, Oregon. They surveyed both north- and southbound whales, observing only on a "sampling" basis during good conditions in daylight hours. Population estimates were made from southbound counts only. Raw counts were 253 in 1979–1980 and 653 in 1980–1981 (actual effort was not reported). Estimates for 1980 ranged from 13,627 to 21,854, depending upon factors corrected for. The minimal figure considered whales missed due to lack of effort during all night and some daylight hours. The maximal figure included corrections for underestimating pod size and whales missed offshore.

During 1980 and 1981, Poole (1984; Chapter 16, this volume) conducted censuses of northbound migrants from Point Piedras Blancas along the central California coast, just north of San Simeon. In 1980, 1,496 whales were sighted during 659 hours of effort; during 1981, 3,296 were seen during 755 hours. Population estimates of 15,725 and 16,140 included corrections for whales passing at night, bias in estimating pod size, and whales passing too far offshore to be seen.

In 1981, Hessing (1983) conducted the second spring census at Unimak Pass. Between March 23 and June 17, 3,851 whales were sighted. From 2 to 10 of ~18 daylight hours were censused each day. Hessing estimated that 14,146 whales passed into the Bering Sea in 1981. A constant night travel rate was assumed, and no corrections were made for poor visibility conditions or for whales passing before and after the census.

ASSUMPTIONS AND SUMMARY OF CURRENT STATUS

Five major topics must be quantitatively addressed in order to estimate population size from shore station counts of migrating whales [Appendix B; see Reilly *et al.* (1983) for a more complete discussion].

Offshore Distribution

Most recent shore censuses have included verification of the offshore distribution of passing whales via aerial surveys [see "History and Methods" (Migratory Route)]. The offshore distribution appears to change during the course of the migration, both southbound (Reilly *et al.*, 1980) and northbound (Chapter 16, this volume). Consequently it is important that aerial observations be compared only to shore observations made at roughly the same time. Observers to date have assumed that all pods passing within some fixed distances are seen. The proportion assumed missed outside of this zone is corrected for by comparing the inshore proportions seen from aircraft and land. At Monterey the results indicated about 20% were missed for this reason (Reilly *et al.*, 1983); for the Newport, Oregon counts the estimate was 38% (Chapter 13, this volume); for Piedras Blancas, 28% during "phase a" only (Poole, 1984). For Unimak Pass in autumn, it was shown that few if any whales were missed solely as a function of their distance offshore (Chapter 10, this volume).

Migratory Timing

To quantify migratory timing, we fit a probability density function to the observed daily Monterey counts, for each year individually. This was useful to compare annual timing between years at one location and between locations for any one year. In assessment, the timing models were used to estimate population proportions passing on days with poor visibility (next section) and on days before and after the censuses.

For the Monterey censuses, extrapolations for whales passing before and after the field efforts increased the total estimates only by ~5% per year. For other censuses which cover a smaller proportion of the migration, estimating the tails is of greater importance. Rugh (Chapter 10, this volume) compared a core period of days between two years, estimating the tails of the earlier, less well-covered year by the ratio of the core periods (but did not estimate total abundance for the earlier year). Poole (Chapter 16, this volume) used a similar procedure for 2 years' data from Point Piedras Blancas. Herzing and Mate (Chapter 13, this volume) did not account for missed "tails" but their censuses may have been long enough for this not to matter.

Visibility Conditions

Lack of fit of the Monterey migratory timing models for any 1 day (after finding model parameters that produced the best overall fit) was highly correlated with visibility conditions, recorded in an ordinal scale (Reilly *et al.*, 1983). For days with conditions worse than "fair" on average, the predicted values from the probability function were used instead of the raw data to estimate the number of whales passing. If in fact there are daily pulses of whales passing the site, independent of weather, this method may bias the resulting estimate. The direction such a bias would take is difficult to predict.

Rugh (Chapter 10, this volume) used an empirical approximation of this method for the Unimak Pass data but worked on a finer time scale of hours rather than days. He noted drops in hourly rate by visibility code and corrected data from hours of "poor" and "unacceptable" conditions by interpolating between periods before and after. Others have used variations of this same technique (Rice, 1961; Poole, 1984; Chapter 13, this volume).

There should be no additional problems in resulting estimates of total abundance from the above visibility corrections, unless gray whales actually slow down during periods of poor visibility (as suggested by R. M. Gilmore, personal communication). If this is so, we are all overestimating population size by some amount which would vary by the method used and the amount of poor weather for which correction was made. The variance of the Monterey estimates increased proportionately with the number of poor visibility days, so this is at least partially reflected in the results for that site. Rugh (Chapter 10, this volume) used deviations from migratory course to suggest that gray whales do not slow down as a function of elevated Beaufort conditions. Perhaps some radio tracking or other electronic-based observation could help clear up the remaining ambiguity on this point.

Observer Accuracy and Precision

When an observer at a shore-based counting station records the passing of a whale or pod, at least two estimates are usually made: the number of individuals present and their distance offshore. To test a sample of "whale counters" for systematic biases in the above estimates, experiments were conducted at the Granite Canyon site during the 1978–1979 migration, involving independent estimates from a mixture of experienced and naive observers for 50 events of passing whales. Results from these experiments included (1) People vary widely in their accuracy and precision in estimating both number and distance; (2) even considering this variability, there are consistent (i.e., significant) biases for both estimates; (3) there is no benefit from experience in accuracy of distance estimation, although there is some benefit in precision. That is, over time a person is likely to become consistent in his inaccuracy if it exists (Reilly, 1981; Reilly *et al.*, 1980, 1983).

Correction for whales missed offshore (Section III,C,1) is confounded by any systematic inaccuracy in estimating distance to passing whales. For the Monterey data, such inaccuracy was detected and corrected for by redistributing the observed data according to results of the observer bias experiments. The overall change in the Monterey population estimates as a result of this correction was quite small. There are potential problems even with this correction before correction, relating to the range of between observer variability. This is discussed further in the following section.

Some results from the Monterey observer bias experiments have been applied to other surveys (Poole, 1984; Chapter 13, this volume). There are two possible problems with this, the first applicable to our original use as well. First, the "sample" of people was relatively small (12, 3 experienced and 9 naive). Second, the sample size of observed pods (50) was not large enough to allow partitioning of pod size estimates by distance to test for interaction. If such interaction exists, the results may not be applicable to sites with migratory corridors significantly different than those at the Monterey sites.

Night Travel Rate

The very limited data applicable to the determination of night travel rate were reviewed in Reilly *et al.* (1980) and Reilly (1981). Only indirect evidence exists: There are no systematically collected data of sufficient sample size which unequivocally measure night travel rate during migration. The indirect information available is more suggestive of a constant 24-hr rate than not, and most recent studies have assumed this (Reilly *et al.*, 1983; Poole, 1984; Chapter 13, this volume; Rugh and Braham, 1979). Rugh (Chapter 10, this volume) collected data using night-vision goggles at Unimak Pass. (These were not useful at Monterey because the whales were farther offshore there.) Two slightly different experiments were run during dusk, comparing sightings made with and without the goggles. These gave two different results. The whales either maintained their daytime rate or slowed to about 73% of that rate. Rugh chose the latter result in computing total abundance. Gilmore (1960, and personal communication) feels that gray whales slow at night in response to limited visual cues for orientation.

Because it is necessary to interpolate more than one-third to two-thirds of the total migration due to darkness (depending on season and latitude), estimation of whales passing at night is the single most important aspect of inferring abundance from shore counts. To date, it is not clear what migrating gray whales do at night or if this behavior changes between locations or between seasons. Considering the relative importance of this, and the relative paucity of our knowledge, it is instructive to investigate how our total estimates would change if gray whales slowed their travel rate at night by various hypothetical amounts. This topic is pursued in the following section.

Discussion

Both the winter range and in-migration censuses require further research before we can be reasonably assured of the accuracy of our population estimates. As stated, my personal bias favors the present estimates from shore counts over those from the winter range. Aside from this, there are reasonable scenarios in which the data from the two sites can indicate similar population estimates.

The following is an exercise in the nature of "what if"? It is not intended as a postulation that the true population size is at any particular value intermediate between shore and winter range estimates. Rather, I wish to demonstrate that within the regions of our uncertainty about night migration rate and the overall accuracy of winter range estimates, there are population sizes that are consistent with data from both sources.

All of the recent shore count estimates are relatively close, about 15,000 to 20,000 for 1980. This is not surprising in view of the essentially common assumptions and corrections used. If gray whales do slow down at night, our data would indicate a smaller population. I have used the 1980 Monterey estimate of 15,647 as an example to indicate how the population estimate would be reduced as a function of a reduced night travel rate (Table III). For example, if the animals traveled at 75% of the day rate, the estimate would be about 13,365. It is logically possible that gray whales speed up their

Table III
Total Population Size Estimates for 1980 from the Monterey Shore Census, as a Function of Hypothetical Night Travel Rates

If night rate is this proportion of day rate	The 1980 population estimate is
1.00	15,647
0.75	13,647
0.67	12,635
0.50	11,083
0.33	9,532
0.25	8,801
0.10	7,432[a]

[a] The 1980 winter range estimate from Rice *et al.* (1983) is 7,601.

rate of travel at night, rather than slowing or maintaining the daylight rate. I can think of no reason why this would be probable and therefore have not pursued an increase in rate in Table III.

In spite of the assumption that night travel is reduced to 73% of the day rate at Unimak Pass in the fall, Rugh (Chapter 10, this volume) produced a 1978 estimate of 17,648 from a maximum raw count of 5,050. This may be increased evidence in support of the magnitude of other shore census estimates but does not clarify the issue of night travel rate. There are other possible ways in which his methods could result in an overestimate, but the amount would be minimal. Previously discussed ways include the possibly inappropriate application of the Monterey pod-size adjustment (because whales pass closer to shore at Unimak, accurate estimation of pod size may be less of a problem there), and Rugh's method of correcting for whales missed in periods of poor visibility. But, if these two corrections are removed entirely, his estimate would still be more than 15,000. It is perhaps relevant to note that the average daylight period is almost 8 hr at Unimak Pass during the fall migration, whereas it is about 10 hr at Monterey. Rugh consequently had a larger proportion of the day over which to extrapolate.

The present status of population estimation from the winter range suggests that 7,600 adults (from the 1981 effort) is an underestimate. These efforts are substantially limited by the physiographic vastness and complexity of the study area. This is exacerbated by the protracted migration into and out of the area, such that the entire population is not present at any one time. Other factors pointing to an underestimate from the winter range are that airplane censuses systematically miss whales (this has not been consistently accounted for), and that the observed ratio of calves to adults from the 1981 survey (Rice *et al.*, 1983) implies a reproductive rate higher than that which gray whales are likely to achieve under any conditions.

The ratio of calves to adults from the 1981 count was 0.19 (Rice *et al.*, 1983). If our current interpretation of gray whale vital rates and age structure is reasonably accurate (Rice and Wolman, 1971; Reilly, 1984) a crude birth rate greater than 0.14 is quite unlikely. This is calculated from a pregnancy rate of 0.467, a sex ratio of 0.5, and a mortality schedule that results in 60% mature ($0.467 \times 0.5 \times 0.6 = 0.14$). If we assume that Rice *et al.* (1983) gave an accurate calf estimate, then 1,439 calves and a maximum crude birth rate of 0.14 indicate a minimum adult population of 10,279. Summing adults and calves gives 11,718. Removing ~7% for 1 year mortality (from 0.10 net for whales under the age of sexual maturity and ~0.05 for those over that age; Reilly, 1984) gives a minimum figure of about 10,900 passing central California the next autumn. If in fact the calf estimate is low, for example, 30% (as suggested by the data of Swartz and Jones, Chapter 14, this volume), then the number passing Monterey would be approximately 14,300. This is within the 95% confidence limits for the 1980 Monterey census (Reilly *et al.*, 1983).

Again, I am not postulating that the population size is exactly 14,300, or that gray whales do in fact slow down at night. Lacking new evidence, it still seems most probable that the night travel rate is on average not different from the daytime rate, and therefore that the population size in 1980 was approximately 15,600. The most important point here is that the Baja estimate is probably an underestimate of total population size. Also, if *not* accurate, the shore station estimates are probably too high. Perhaps research in some key areas will help us reinterpret our census data and result in a resolution to the present dilemma. Unequivocal documentation of night travel rates during migration is needed. Further field work on the winter grounds, directed at verification of specific problem areas and coupled with a comprehensive, quantitative appraisal of the entire estimation problem there, are prerequisite to reliable population estimation.

Appendix A. Factors Affecting or Involved in Estimating Total Abundance from Winter Range Aerial Surveys

I. Specific research topics
  A. Behavior of animals
    1. Time spent at the surface
      a. Age/sex group differences
      b. Group size differences
      c. Location differences
      d. Diel differences
      e. Intraseason changes
      f. Response to platform
    2. Immigration emigration
      Same factor list as in 1. above
  B. Geographic distribution
    1. Lagoon channel
    2. Lagoon mouth
    3. Lagoon open area
    4. Alongshore bay

        5. Alongshore exposed, sandy beach
        6. Alongshore exposed, rocky beach
    C. Interplatform comparisons
        1. Lagoons
            a. Air to boat
            b. Air to tower
            c. Boat to tower
        2. Alongshore
            a. Air to boat
    D. Visibility conditions
        1. Quantity (scale effects)
        2. Confounding with behavior?
        3. Confounding with field methods?
    E. Observer accuracy and precision
        1. Experience
        2. Fatigue
        3. Intraobserver variation
        4. Interobserver variation
II. Methods
    A. Field methods
        1. Altitude
        2. Air speed
        3. Location
        4. Track line repetition
        5. Data recording
        6. Intraseason timing
        7. Boat, land-based verification experiments
    B. Analytic methods
        1. Post factor stratification, pooling
        2. Sighting model definition
        3. Parameter estimation
        4. Parameter comparison
            i. Between platforms
            ii. Between locations
            iii. Between observers
        5. Data, parameter "adjustment" (i.e., application of correction factors)
        6. Estimation of total abundance and variance
            i. Model derivation
            ii. Computation conventions

Appendix B. Factors Affecting or Involved in Estimating Total Abundance from Shore Station Censuses for Migrating Whales

I. Specific research topics
  A. Offshore distribution
    1. Site characteristics
    2. Season
      a. Between (fall versus spring) changes
      b. Within-season changes
    3. Group size differences
  B. Migratory timing
    1. Model estimation
    2. Comparisons between years
    3. Comparisons between sites
    4. Estimation of "tails"
    5. Estimation of poor visibility periods
  C. Visibility conditions
    1. Establish scale of effect
    2. Confounding with A., B.
  D. Observer accuracy and precision
    1. Distance estimation
      a. Change with distance?
      b. Change with pod size?
    2. Pod size estimation
      a. Change with distance?
      b. Change with pod size?
    3. Interobserver differences
    4. Intraobserver differences
  E. Diel migration rate
    1. Night versus day rates
    2. Change during daytime?
II. Methods
  A. Field methods
    1. Site choice
    2. Data collection conventions (i.e., variables chosen, frequency recorded, etc.)
    3. Verification experiments (for distance, pod size)
  B. Analytic methods
    1. Post facto stratification, pooling (distance only)
    2. Parameter estimation
      a. Distance offshore
      b. Pod size
      c. Number per time interval

3. Parameter adjustment (re: verification experiments)
   a. Offshore distribution
   b. Pod size
4. Estimation of total abundance and variance
   a. Model derivation
   b. Computation conventions

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Observed and Maximum Rates of Increase in Gray Whales, *Eschrichtius robustus*

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ABSTRACT

Shore station censuses indicate that the California stock of gray whales increased at an annual rate of 2.5% during 1967–1980, concurrent with an annual exploitation of approximately 1.2%, i.e. net reproduction was near 3.7% per year. In light of this net reproduction, vital-rate estimates for the *circa* 1967 population were re-evaluated. The most likely values during that period were: pregnancy rate of 0.467, mean age at sexual maturity of 8 years, adult survival of 0.945 and juvenile survival of 0.899. To estimate maximum net rate of increase, biologically defined limits of pregnancy rate, age at sexual maturation and juvenile survival were used to generate a Leslie matrix, with adult survival held constant at the 1967 level. The dominant eigenvalue of the matrix was calculated as 1.069. If a stable age structure can be assumed in populations at a very low level, this indicates a possible maximum net rate of increase approaching 6.7% per year.

INTRODUCTION

In the study of animal population biology the rate of increase exhibited by a reproductive stock is of interest in both applied and theoretical contexts. The maximum possible, or intrinsic rate of increase, and the realized rate under a set of definable and measurable conditions have relevance both for the study of population dynamics in general and for the management of exploited mammal populations.

In this study I have estimated the maximum rate of increase for the California stock of gray whales from what is known or can be inferred of the stock's vital rates, utilizing a population projection matrix. The observed rate of increase was calculated directly from data collected during annual shore station censuses. In the course of estimating the rates of increase, our state of knowledge of much of the reproductive biology of the stock has been reviewed, with new estimates made for some vital rates. Dependence of the rate of increase on population density or some related factor is tacitly assumed here. Data do not presently exist to test this assumption for gray whales.

Observed rate of increase, as measured through sighting censuses, is addressed here first. All available time series of sighting censuses were reviewed for applicability as indices of change in population size. Results from this section are then utilized in the following sections, in the estimation of vital rates and finally of maximum rate of increase. These results have potential interest in interpreting the assumed 'recovery' of the stock from severe depletion, in evaluating the effects of contemporary exploitation by the Soviet subsistence fishery, and in estimating the potential impact of major perturbations resulting from natural or man-induced changes on the calving and feeding grounds.

As part of their monographic study, Rice and Wolman (1971) reviewed information available up to 1970 on rate of increase. From Point Loma censuses of the 1950s they estimated an annual increase of 12.2%. This is re-estimated below. Rice and Wolman (1971) also estimated an annual rate of increase of 0.8% from the 1954–1964 Baja lagoon censuses. These data are also reviewed here.

Chapman (1981) estimated observed rate of increase from two of the time series examined here: early Pt Loma shore counts (10.4%) and Baja lagoon aerial counts (8.0%).

Previous studies which treated gray whale vital rates include Blokhin (1979; 1982), Ohsumi (1976), Rice and Wolman (1971), Zenkovich (1934; 1937), Zimushko (1969a; 1969b; 1970; 1971; 1973) and Zimushko and Ivashin (1980). Findings from these studies are reviewed below, with new estimates produced in some cases.

DATA SOURCES

Sighting time series

Data exist from four series of censuses of gray whale population size: three from shore-based counts of southbound migrating whales and one from aerial censuses of whales on their winter grounds along Baja California. For two of the four with interpretable data, rate of increase was estimated using exponential regression techniques.

Vital rates

Two data sources exist for the estimation of gray whale vital rates: from a series of whales examined by Rice and Wolman (1971) during the 1960s and from animals examined in the Soviet subsistence fishery during the 1960s, early 1970s and 1978–1980.

During 1959 through 1969 Rice and Wolman (1971) examined 316 gray whales collected off the coast of central California, between Half Moon Bay (37° 30′ N) and Point Reyes (39° 00′ N). Whales were captured *en route* both north and south (Table 1). The majority of collections were made during 1964 through 1969, with a mean collection date of 1967. For vital rate estimation, in both Rice and Wolman's analysis and here, the entire series was pooled over collection years in order to maximize sample sizes. It is possible that one or all vital

Table 1

Dates of capture for 316 gray whales collected off the central coast of California for Rice and Wolman (1971), used here for estimation of vital rates

Dates	Number of whales taken	Direction of migration
23–26 Feb. 1959	2	North
23–30 Mar. 1962	4	North
14–25 Mar. 1964	20	North
22–29 Mar. 1966	26	North
14 Dec. 1966–19 Jan. 1967	95	South
21 Feb.–9 Mar. 1967	30	North
14–25 Jan. 1968	35	South
26 Feb.–11 Mar. 1968	24	North
2–11 Apr. 1968	7	North
20 Dec. 1968–9 Jan. 1969	50	South
2–16 Mar. 1969	23	North

rates changed during the 10 years sampled (1959–69). If so, statistics estimated from the pooled data are at best representative of the mean rates and may also be biased.

Ohsumi (1976) utilized the Rice and Wolman (1971) estimates of pregnancy rate, age at sexual maturity and adult mortality in a simulation study. He estimated juvenile mortality from their data using a simple balance equation. An alternative method to estimate juvenile mortality is proposed below.

Soviet scientists have examined a sample of animals taken in the subsistence fishery in the Bering and Chukchi Seas. A limited amount of information has been reported in a number of short communications. For the years since 1948, total Soviet landings have been reported (Ivashin and Mineev, 1981; Blokhin, 1979; 1982). For 1965 through 1980, sex ratio and proportion mature of landed animals have been reported (Zimushko and Ivashin, 1980; Blokhin, 1982) (Table 2). Frequencies of pregnant females were reported for 1965–1970 (Zimushko, 1969a) and 1978–1980 (Blokhin, 1982). Zenkovich (1937) listed some information on pregnancies from a 1933–1936 series of Bering/Chukchi Sea specimens. For growth and related parameters, analyses and conclusions with varying and limited amounts of supporting data have been published (Zimushko, 1969a; 1969b; 1970; 1971; 1973; Zimushko and Ivashin, 1980; Blokhin, 1979; 1982).

The 1965–70 series of vital-rate estimates from the Soviet data represent roughly the same time period as the Rice and Wolman series and should be comparable from that standpoint. For 1978–1980 the proportion of mature females which were pregnant in catch sub-samples was reported (Blokhin, 1982). Sample sizes were given only for the 1980 data.

Below I review comparative estimates for pregnancy rate, age at sexual maturation, adult and juvenile survival (mortality) rates. New estimates are made here for all but age at sexual maturation.

METHODS

Age determination

As with other baleen whales, earplug laminae have been the primary measure of age in gray whales (Rice and Wolman, 1971; Zimushko, 1973). For adult females, ovarian corpora have also been used. Both time scales are subject to assumptions that are partially or totally untested, including regularity in time of deposition of marks and persistence of marks throughout life. Rice and Wolman estimated that one earplug layer was deposited per year, except for the first year of life, when two layers were deposited. Their interpretation is followed here.

The one-year pattern is in agreement with Roe's (1967) conclusions for fin whales. Zimushko (1969a 1969b; 1971; 1973), however, suggested that two layers per year were deposited in gray whales. This interpretation implied a halved life span (about 30 years at most), sexual maturation at 4.5 years with a minimum of 3 years, and a doubled ovulation rate (in relation to Rice and Wolman's interpretation). In later Soviet papers (Zimushko and Ivashin, 1980; Blokhin, 1979; 1982) the two-layers-per-year interpretation is no longer cited. Lacking new information, the interpretation of Rice and Wolman appears to be the most reasonable.

Notable problems with earplug ageing of gray whales are that the plugs are 'readable' in only about half of the individuals and that there may be fading of juvenile-deposited layers in later life (Rice and Wolman, 1971). Because of these problems, Rice and Wolman used the frequency of corpora in the ovaries of adult females as an alternate scale (discussed below).

Vital rates

Adult survival was estimated in this study and by Rice and Wolman (1971) using the methods of Chapman and Robson (1960). Alternate estimates with older whales truncated were made here in response to Rice and Wolman's (1971) concern that age determination of these 'older' whales was relatively imprecise.

Indirect methods must be employed to estimate juvenile survival. This is because in both the Soviet fishery (Zimushko and Ivashin, 1980) and probably to a lesser extent in the California scientific collections (Rice and Wolman, 1971) juvenile whales were selected against.

Table 2

Gray whales captured in the Soviet subsistence fishery from the Bering and Chukchi Seas, which were sampled for (at least) measurement and sex identification. From Zimushko and Ivashin (1980) and Blokhin (1982)

		1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79[1]	80
Adult	F	47	16	16	31	11	56	1	21	73	74	73	84	4	8	?	44
Juvenile	F	41	2	8	1	2	10	1	1	4	14	40	11	6	7	?	26
Adult	M	39	19	30	10	4	69	2	3	89	80	30	57	?	?	?	19
Juvenile	M	17	4	10	6	1	6	0	0	6	11	28	11	?	?	?	9
Total no.		144	41	64	48	18	141	4	25	172	179	171	163	19	31	?	98

[1] For 1979 the sample size examined for age/sex status was not reported.

Prior to conducting his simulation of population trends, Ohsumi (1976, Equation 4) estimated juvenile mortality (where mortality is the negative logarithm of survival) using a two-age-class balance equation (also occasionally used by the International Whaling Commission's Scientific Committee):

$$1-e^{-(M+F)} = (P/2)\,e^{-(M'+F)\,X_m}$$

where M' = juvenile mortality, M = adult mortality, P = pregnancy rate, F = fishing mortality and X_m = age at sexual maturation. This model assumes no net recruitment, equal vulnerability of juveniles and adults to fishing death, and population lumped into two age classes. Since we have estimates of gray-whale population growth and the range of ages during which sexual maturity is attained, it is possible to estimate juvenile survival more accurately, using this additional information.

As an alternative balance model to estimate juvenile survival, I have used a Leslie (1945) population-projection matrix,[1]

$$L = \begin{Bmatrix} f_0 & f_1 & \ldots & f_k \\ S_0 & 0 & \ldots & 0 \\ 0 & S_1 & \ldots & 0 \\ 0 & 0 & .\,S_{k-1} & 0 \end{Bmatrix}$$

where the elements of the top row are age-specific fecundities, the elements of the subdiagonal are age-specific survivals, and $k+1$ specifies the number of age classes. Here $k+1$ was set at 40, since approximately 98% of the population is 40 or younger (Rice and Wolman, 1971). Rate of increase can be dealt with implicitly when using a Leslie matrix, since the dominant eigenvalue λ (see Leslie, 1945) is the antilog of rate increase: $\lambda = e^r$.

With values set for λ, f (fecundity vector) and adult survival, the characteristic equation for the Leslie matrix can be solved iteratively for S_0, the juvenile survival rate.

Even when only estimates of 'juvenile' and 'adult' rates exist, if a distribution of transition proportions between juvenile and adult stages can be approximated, recruitment to sexual maturity can be reflected as a gradual process. This introduces some of the advantages of a fully age-structured model.

In employing this age-structured technique, rates were assumed constant over large series of ages, i.e. 0–4 years for juveniles, 12+ years for adults. For the apparent transition period of 5–11 years of age, both fecundity and survival rates were changed gradually. The cut-points were defined by the age-at-sexual-maturation data, described in Vital Rates. To accomplish this, a function approximating the proportion of each age class sexually mature was defined, for a = age and x_m = median age at maturity, as

$$f(a) = \begin{cases} 0 & a = 0, 4 \\ (a-5)\cdot(0.5/X_m-5) & a = 5, X_m \\ 0.5+(11-a)\cdot(0.5/11-X_m) & a = X_m+1, 11 \\ 1.0 & a > 11 \end{cases}$$

The result is a vector r with elements on the interval (0, 1) which are the proportions of each age group sexually mature, and $f(a)$ set at 0.5 at the defined age at sexual maturation X_m. Fig. 1 illustrates the vector r for three values of age at maturation (X_m). The vector of age-specific fecundities was then generated by multiplying r by half the pregnancy rate and by juvenile survival, to estimate female young surviving through their birth year:

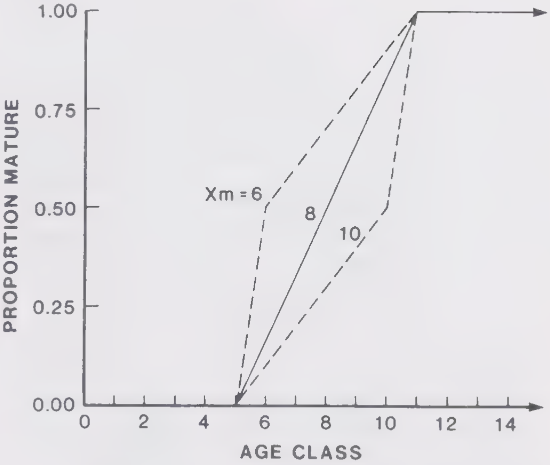

Fig. 1. Examples of vectors of proportions of each age class mature, for mean ages at sexual maturity of 6, 8 and 10 years.

$$f = r\cdot(P/2)\cdot S_j$$

The vector of age-specific survivals (s) was generated by defining a transition between juvenile (S_j) and adult survival (S_a) as

$$s = (S_a\cdot r)+[S_j\cdot(1-r)].$$

(In the current use, we are attempting to estimate S_j).

The gradual recruitment of age classes to the mature population during the transition years 5 through 11 is a closer representation of variability to be expected in the process of maturation in a mammalian population than simple knife-edged recruitment. To complete the procedure, a Leslie matrix (2) was defined using s and f.

Juvenile survival (S_j) was estimated by setting S_a, P, X_m and λ, and iteratively changing S_j until the characteristic equation for (2) was solved for λ to within a minimum tolerance of 0.001.

Rate of increase

Maximum rate of increase was also estimated using the Leslie matrix. To accomplish this, S_j, P, and X_m were set at values which were identified here as biological limits that would be approached as population density approached zero, assuming that these vital rates are variable in a density-dependent manner. Adult survival (S_a) was assumed not to be density-dependent here, following the arguments of Fowler (1981) and Eberhardt and Siniff (1977). The maximum rate of increase was then calculated from the dominant eigenvalue of the resulting matrix.

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[1] Other, simpler methods could be used to estimate juvenile survival here, e.g. a Leslie matrix with all fully adult age classes collapsed into one term. The full matrix approach was used for consistency with a larger, complementary study (Reilly, 1981) in which population projection was done.

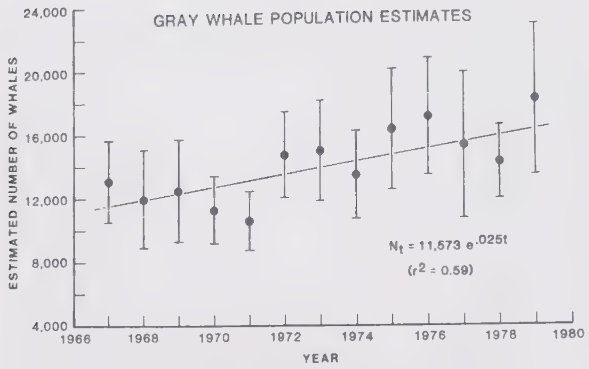

Fig. 2. Gray-whale population estimates and 95% confidence limits from Monterey shore censuses, 1967–68 through 1979–80.

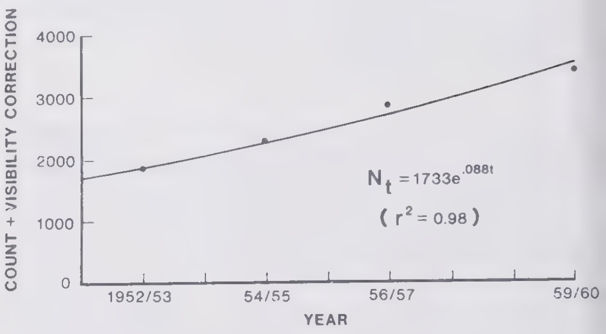

Fig. 3. Gray-whale population estimates from four Point Loma shore censuses during the 1950s.

SIGHTING TIME SERIES: OBSERVED RATES OF INCREASE

Monterey shore censuses

Of the four time series of sighting-census data, the Monterey shore censuses appear to be the best for measuring the rate of change in population size. This is because it is a series of 13 consecutive censuses (1967–68 through 1979–80) of southbound migrants, during which consistent and well documented counting and data recording methods were used. Also, annual variability, due to changing weather and visibility conditions, and intra- and interobserver biases were addressed at least in part (Reilly, Rice and Wolman, 1980; 1983). A potential limitation of this series as an index of change in population size is that the census site was moved a few miles south from the original location after the seventh year. However, the two sites were very similar in seaward sighting perspective, and the data showed no significant differences between locations; group size distributions recorded at the two stations were not different, and the offshore distance distributions showed much less variation between locations than between years at either location (Reilly *et al.*, 1980; 1983).

The rate of change in population size during the 13 years censused was 2.5% per year (S.E. = 0.96) (Fig. 2). When the approximately 1.2% annual harvest in the Soviet subsistence fishery during these same years is also considered, an annual net reproduction of near 3.7% is indicated. (The term 'net reproduction' is used here to describe net rate of increase plus removals by humans).

Hubbs/Scripps shore censuses

Beginning in 1946–47 at the Scripps Institution of Oceanography (near San Diego, California) students under the direction of Carl L. Hubbs were stationed on top of a classroom building. The amount of effort and the methods applied are not clear from the secondhand accounts available (Walker, 1949; Gilmore, 1960). The recorded counts in 1946–47 through 1951–52 (omitting 1950–51) were 250, 500, 600 and 800. An increase is clear. If the methods and efforts were fairly constant (which is doubtful, given the 100% increase in the 2nd year) and if the migration corridor was unchanged during this time, an exponential rate of increase of 20% per year was occurring. This seems unlikely. I consider these data unreliable, having so little accompanying information on effort expended and methods used.

Early Point Loma shore censuses

Beginning in 1952–53 a census of southbound migrants was conducted from Point Loma (San Diego, California) intermittently until 1959–60. Gilmore (1960), who supervised the efforts, eliminated two of the first five annual counts from consideration, due to irregularity of methods and/or effort. Rice (1961) reported the results of the final (1959–60) count for the series. The value of these data as an index is contingent upon the validity of Gilmore's (1960) and Rice's (1961) schemes to correct for whales missed due to poor visibility. Gilmore (1960) subjectively estimated the percent reduction in visibility each day to upwardly adjust his counts, while Rice (1961) drew a smooth curve on a figure connecting the higher count days. Consequently, the data from 1959–60 are not strictly comparable to those from previous years.

Another problem with the Point Loma data, perhaps the most serious, is the likelihood that the proportion of the population passing close enough to shore to be seen changed throughout the years covered, due to increasing nearshore boat traffic (Rice, 1965; Reeves, 1977; Gilmore, 1978). If one were to disregard the above inconsistencies and use the four 'good' censuses from the 1950s to estimate the rate of change during the decade, an exponential rate of 8.8% per year is indicated (Fig. 3). This is lower than Chapman's (1981) estimate (10.4%) because he used the authors' final population estimates (which include further unstandardized corrections) rather than just the raw data corrected for visibility as used here. Rice and Wolman's (1971) estimate of 12.2% annual increase from the same data probably represents a miscalculation.

There were five further censuses conducted at Point Loma intermittently between 1967–68 and 1978–79. These were not analyzed in detail by Reilly *et al.* (1980; 1983) due to the above unaddressed questions regarding the distribution of, and changes in, the migratory corridor. Further, the methods used during the later Point Loma series differed somewhat from the early efforts there and are therefore not reasonably considered as part of a single time series.

Baja lagoon aerial censuses

There have been a number of aerial counts conducted on the winter grounds during the past 30 years. These were begun in 1952 by Carl L. and Laura Hubbs, and repeated by them and others during most years through 1964 (Hubbs and Hubbs, 1967; Gilmore, 1960). Gard (1974; 1978) conducted similar counts during 1970, '73, '74, '75, and '76. Recently, Rice, Wolman, Withrow and Fleischer (1981) and Rice, Wolman and Withrow (manuscript) conducted aerial counts on the winter grounds in 1980 and 1981, respectively.

As with the early shore censuses, the aerial counts were not conducted in a consistent manner. As discussed by Rice *et al.* (manuscript), reliable estimates from aerial counts in and outside the calving lagoons can be obtained only if many replicate surveys are made within a short time period, at the same time each year, along standardized census tracks at standardized altitude and speed, under good visibility conditions. With the exception of the very latest, none of the annual aerial surveys meet any of the requirements, except that most were conducted sometime during February. Rice *et al.* (manuscript) feel that these early efforts are consequently, 'worthless for estimating population sizes and trends'. Consequently, no rate of increase estimates are produced here from the lagoon aerial counts. Previously published estimates from this series include 0.8% per year (1954–64, $n = 4$, Rice and Wolman, 1971), and 8.0% (1952–59, $n = 4$, Chapman, 1981).

In summary, of four available time series of gray whale sighting surveys, only one is reliable enough to allow estimation of rate of change in population size: the Monterey 13-year series. The early Scripps series are not interpretable given present information. The 1950s Point Loma counts are of questionable value as an index of change due to unstandardized methodology. The Baja Lagoon aerial counts have even more severe methodological inconsistencies. The Point Loma series from the 1950s, perhaps the most reliable of the three sources other than Monterey, indicates a rate of increase of 8.8% per year. The possibility of the population achieving an 8.8% per year rate of increase is considered below in relation to vital rate estimates.

VITAL RATES AND MAXIMUM RATE OF INCREASE

In this section I review available information pertinent to gray whale vital rates, present slightly different estimates for the *circa*-1967 pregnancy rate and adult and juvenile mortality and use the existing estimate for age at sexual maturation. Then, the maximum rate of increase is inferred from the vital-rate values assumed for the near-zero population level, by use of a Leslie matrix. This rate is an estimate of the asymptotic or potential for the population, equivalent to r_s of Caughley (1977).

Age at sexual maturity

Both Rice and Wolman (1971) and Zimushko (1969a; 1971) used evidence of ovulation or pregnancy as evidence of maturity in females. Rice and Wolman found immature females with as many as 12 earplug layers and mature ones with as few as six. The median number of layers at maturity was nine. Zimushko also concluded that nine layers was the approximate time of attainment of maturity for females. The minimum number of layers in a mature female was eight in the Soviet sample, and the maximum in an immature individual was 12. The disparity in minimum layers for maturity was most likely due to sampling error. Only 34 females were examined by Zimushko (1969a), while Rice and Wolman (1971) examined a total of 140 females (not counting fetuses), of which 68 had readable ear plugs.

For the detection of maturity in males, Rice and Wolman relied solely on histological examination of the testes for evidence of spermatogenesis. Zimushko (1969a; 1971) examined a sub-sample histologically (apparently nine of 23, but this is not clear), using percent of seminal ducts open as a criterion of maturity. He combined this with an analysis of growth rate of testes weight to conclude that males reach maturity at approximately 11.1 m in length (Zimushko, 1971). Ranges in numbers of earplug laminae at maturity are not clearly stated for males from these studies. Rice and Wolman found essentially the same timing in males as in females. The median number of earplug layers at maturity was 9, the minimum 6 and the maximum 12.

Following this approach, then, gray whales became sexually mature at a median age of 8 years, a minimum age of 5 years, and a maximum of 11 years.

Population pregnancy rate

The independent data sets available on life history should allow two independent estimates of pregnancy rate for the *circa*-1967 population: one from the summer feeding grounds and one from the migration past central California. There are problems with the estimates produced from both, however. A revised estimate for this time period has been calculated here. Blokhin (1982) reported pregnancy rate statistics from the 1978, 1979, and 1980 harvests. These results are compared below to the pregnancy rate information for the late 1960s. A number of issues relative to an accurate determination of current and maximum pregnancy rate are problematic. These include ovulation rate, accurate ageing (discussed above), length of and possible overlap in gestation and lactation, and sampling biases.

In the sampling of migrating gray whales conducted by Rice and Wolman (1971) one important component of the population was missed due to the timing of the captures (e.g. Poole, 1984): post-partum females with calves of the year. There also appeared to be biases toward late pregnant females captured during the southward migration. Consequently, direct estimation of population pregnancy rate from their data is not possible.

Rice and Wolman (1971) examined a total of 116 mature females (Table 3). Late pregnant females headed south and post-partum females headed north were excluded from their computations of pregnancy rate

Table 3

Reproductive state of sexually mature female gray whales examined by Rice and Wolman (1971), classified by direction of migration

South		North	
Condition	Number	Condition	Number
Late pregnant	56	Post-partum (non-lactating)	2
Recently ovulated	28	Early pregnancy	22
		Resting	8

Table 4

Percent of mature females which were pregnant from Soviet gray-whale catches for four consecutive years (*P*), 1965–1968 from Zimushko (1969), with sample sizes for each year (*n*) inferred from Zimushko and Ivashin (1980; Table 3), and a chi-squared test of differences in proportion pregnant between years

	Year				
	1965	1966	1967	1968	Total
P	46.3%	56.3	33.3	53.1	46.7%
$n(P)$	22	9	9	17	57
$n(\text{not } P)$	25	7	18	15	65

$\chi^2 = 3.055$, d.f. $= 3$, $P = 0.617$ (not significant).

because of the apparent biases mentioned above. They assumed that all 28 recently-ovulated animals headed south had conceived and that the number of females impregnated the previous year (giving birth in the current 'year' and absent from the samples) was approximately equal to the number assumed pregnant in the 'current' year. Consequently, 50 were in effect added to the denominator of the ratio of pregnant to total from the sub-sample (50/58), to produce $P_1 = 50/58+50 = 0.463$.

There are two aspects of Rice and Wolman's pregnancy rate estimation that may be in error. First, the assumption of one pregnant (post-partum) female missed for each 'pregnant' (recently ovulated or early pregnancy) whale in the sample appears valid for northbound captures but not for southbound. Second, it is probably unreasonable to assume that all corpora lutea observed represented pregnancies. Alternative interpretations are possible, but these also require conjecture.

Data from the Soviet fishery may help to clarify the issue of the *circa*-1967 pregnancy rate. Zimushko (1969b) reported percent pregnant by year for four years (1965 through 1968). From Zimushko and Ivashin (1980, Table 3) the sample sizes can be inferred (Table 4). Zimushko (1969b) speculated from this four year series that the proportion pregnant oscillates on a two-year cycle: one year above 50%, one year below. From this he further speculated that only a proportion of the population was on a two-year breeding cycle and that other females gave birth two, three or even four years in a row before resting for a year. Contributing to this picture was Zimushko's early (1969a; 1969b; 1971; 1973) interpretation of ageing, i.e. two layers accumulated per year.

I conducted a chi-squared test of differences in proportions pregnant between years in the Soviet data (Table 4). An hypothesis of equal proportions between years cannot be rejected. Pooling the data over years, then, gives:

$$p_2 = 57/122 = 0.467$$

with variance

$$\begin{aligned} \operatorname{var}(p_2) &= (0.467)(1-0.467)/121 \\ &= 0.00205. \end{aligned}$$

This is quite close to Rice and Wolman's (1971) original estimate (0.463) from the California series. If the sampling was unbiased, this estimate should be a valid representation of the pregnancy rate, being based upon 122 captures of adult females. The 95% confidence limits are (0.376, 0.558).

The variation between years in proportion pregnant in the 1965–1968 data from the summer grounds is possibly due to temporal sampling differences. This is suggested by the data and analyses of Blokhin (1982) for the years 1978–1980. He found a strong decreasing trend in proportion of mature females which were pregnant, by month from July through October, in the Soviet subsistence-fishery captures. The July proportion was near 0.90, declining to near 0.10 in October (Blokhin, 1982; Fig. 2). The overall pregnancy rate during the 3 years is not directly calculable, since the raw data were reported only for 1980. In that year the pregnancy rate was 0.52. For 1978 and 1979 only proportions were reported, without sample sizes: 0.30 for 1978 and 0.84 for 1979. Blokhin mentioned that seasonality was probably responsible for the wide distance between these estimates, sampling for 1978 having been predominantly late in the summer while sampling for 1979 was predominantly early in the summer. The mean of the three proportions is 0.55. It is possible that this is an accurate estimate, but an examination of the components of the calving interval (below) suggests that a rate greater than 0.5 is unlikely. Sampling bias toward pregnant females is suggested here. This also casts some doubt on the accuracy of the earlier summer-range data as well.

It is interesting to note that the proportion pregnant appears to be positively corrected with the proportion sexually mature in the three annual samples reported by Blokhin (1982): 1978 had 46% mature and 30% pregnant; 1979 had 87% and 84%, while 1980 had 63% and 52%. This also suggests that much of the inter-year variation in pregnancy rates is due to sampling problems.

For maximum pregnancy rate (or minimum calving interval), Rice and Wolman (1971) estimated 0.5 (2 years), while Zimushko (1969a; 1969b; 1971) estimated that it is greater than 0.5 (less than 2 years). Apparently these authors had differing interpretations of the components of the calving interval, i.e. length of gestation, and the possibility of overlapping lactation and/or gestation with ovulation. The minimum calving interval biologically possible is an important factor in the estimation of maximum rate of increase. Consequently the separate components of the calving interval are reviewed below.

Lactation period

The lactation period is indicated to be approximately 7 months, from collection dates of weaned calves reported from the summer feeding grounds (Zenkovich, 1937; Tomilin, 1957). Nearly all calves collected during August and later, by the above sources, were weaned, having solid food but no milk in their stomachs. No data exist to examine possible trends in lactation period with time or changing population size.

Gestation period

Rice and Wolman estimated the gestation period to be 13 months, using the curve-fitting method of Hugget and Widdas (1951). This method assumes fetal growth to fall into two phases: an initial slow period followed by a longer, much faster period of growth. The later part of the gestation period is estimated from empirical data on fetal sizes and calendar date. Estimation of the initial phase is not as straightforward. Based upon an analysis of the state of development of two embryos, Rice and Wolman (p. 79) estimated the initial phase to last 75 days. The empirically estimated phase was 325 days, so their estimate of the total period was 400 days, or about 13 months.

Zimushko and Ivashin (1980) approached this situation in a different, slightly more qualitative manner. On a 'circular graph' of months of the year they plotted the sizes of fetuses by month. They concluded that the period is less than 12 months, not 13. Their figure shows the mean conception date to be in mid-February. This is about 11 months from the mean birth date of 20 January (Rice *et al.*, 1981). It appears, however, that Zimushko's technique does not take the initial, slow phase of fetal growth (Laws, 1959) into account. Zimushko's extrapolated conception date (February) is in fact near the date at which the line from the 'linear' growth phase in Rice and Wolman's (1971; Fig. 29) analysis meets the origin. Also, all adult females taken by Rice and Wolman on the southward migration (except those with near-term fetuses) had fresh large corpora lutea. This indicates that they had at least ovulated, if not conceived. No embryos were found in these females. This could have been due to the small size of a new conceptus. Alternatively, all of these individuals could have ovulated again during the same season. This second alternative is not supported by the available data on ovulation rate (see below).

For gestation period, then, available data are not entirely conclusive. More work is desirable on estimation of the early phase of fetal growth. A period somewhat greater than 12 months appears most likely at this time.

Frequency and timing of ovulation

A simple linear regression of number of corpora lutea and c. albicantia vs. number of ear-plug laminae for 49 female gray whales results in the following equation (Table 5; data from Rice and Wolman, 1971):

$$\text{No. corpora} = (0.518)\cdot(\text{no. layers}) - 0.891 \quad (r^2 = 0.614)$$

The slope of 0.518 is not significantly different from 0.5 ($t = 0.334$ $p = 0.65$) (Fig. 4). If multiple sequential ovulations were a common phenomena, a higher rate of ovulation would be expected. These data appear to support the concept of a 2-year minimum breeding cycle. Certainly not all ovulations would result in pregnancies.

Another factor to be considered in determining the length of the female reproductive cycle is the occurrence of either a post-lactation or post-partum ovulation/conception. A post-lactation ovulation/conception appears unlikely, given the relative uniformity in size of fetuses with time of year (Rice and Wolman, 1971; Zimushko and Ivashin, 1980) and the overall fairly precise, annual timing of the gray whale migration schedule. Given that Rice and Wolman (1971) observed no enlarged follicles in ovaries from 56 southbound females with near-term fetuses, a common post-partum ovulation also appears unlikely. It apparently does occur on some occasions, though, since Zimushko (1969a) reported the capture of seven simultaneously lactating and pregnant females from the Soviet fishery. The total sample size from which these seven were drawn was not stated and is difficult to infer from the text. As no near-term females were found to exhibit signs of imminent ovulation from the California specimen series, however, I consider this a relatively uncommon event.

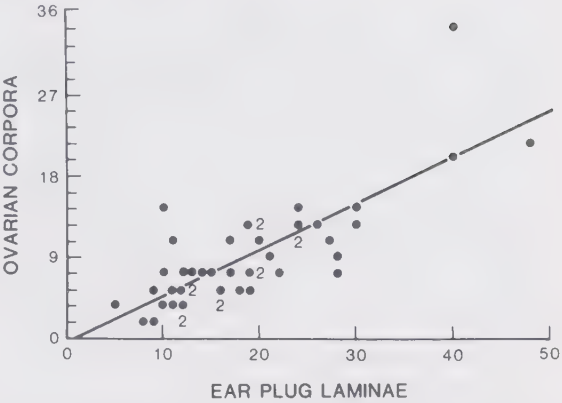

Fig. 4. Relationship between frequencies of ear-plug laminae and ovarian corpora for 49 gray whales. The slope = 0.518 ($r^2 = 0.614$).

When discussing life history characteristics in relation to ovarian scars, it is important to remember that there are still uncertainties involved: (*a*) ovulation may not be a regular, semi-annual event, (*b*) ovulation rate may change with age, and (*c*) it is unknown if all corpora persist throughout life (Perrin and Donovan, 1984).

Age-specific pregnancy rates

Zimushko (1970) examined the ovaries of 70 mature female gray whales. He distinguished two types of corpora albicantia: those of ovulations which had resulted in pregnancy, and those which had not.[2] From this he inferred a declining fecundity with age, as represented by a decreasing ratio of the corpora of pregnancy to those of non-pregnancy in older whales (Zimushko, 1973). No sample size was given for testing this hypothesis. A ratio of 1:1 for whales 12.0–12.5 m long, and 1:2.5 for females of 13.1–13.5 m was reported. A figure was presented by Zimushko (1973) with data for nine points (reproduced in Zimushko and Ivashin, 1980) to illustrate this concept. Unfortunately, the points cannot be read from the figure without conjecture, and

[2] Ivashin (1984) describes methods used by Soviet scientists for classifying corpora

no means of substantiating the changing ratio is available. Regarding the basic premise, that two types of corpora albicantia can be distinguished for gray whales, Rice (pers. comm. 1981) states that Zimushko's method is faulty and that no clear consistent difference exists (see also Perrin and Donovan, 1984; Ivashin, 1984).

Laws (1961) could distinguish no such differences in fin whale corpora. Mizroch (1981) found no decline in proportion pregnant with age in an analysis of a large series of Southern Hemisphere baleen whale reproductive data. I have assumed fecundity constant for adult (beyond 11 years of age) gray whales, lacking conclusive evidence to the contrary. This controversy is not likely to be settled without substantial histological research on gray whale corpora.

In summary, neither the pregnancy rates for *circa*-1967 and 1978–80 nor maximum pregnancy rates can be unambiguously determined from available information. The data on ovulation rate and ovarian condition of southbound migrating females point to a two-year minimum cycle. It is not entirely clear what the gestation period is, but the best available data point to a period greater than 12 months, also supporting a two-year minimum cycle. The report of seven simultaneously pregnant and lactating females captured from the feeding grounds (Zimushko, 1969a) bears further verification, including accessory data on the size of the sample from which these were drawn. They point to an inconsistency in our understanding of gray whale reproductive biology as yet unresolved.

Adult survival rate

The Rice and Wolman (1971) samples provided the only information available on adult survival rate (S_a). From their data (Table 5), apparent adult survival rate (A) can be estimated from the frequencies of individuals per age class. If the population is stable in age structure, stationary in size and has not been subject to exploitation, this should be an unbiased estimate of adult survival. The California stock of gray whales had most likely been under exploitation continually since pre-history (Mitchell, 1979). There is no way of knowing if the age structure was stable in the mid 1960s, but the population was probably increasing in size. Consequently, while apparent survival (A) has been estimated with some degree of certainty here, the proportions of this estimate ascribable to growth (G) and exploitation (F) are less certain.

Rice and Wolman preferred the use of ovarian corpora to estimate apparent adult female survival and reported a Chapman–Robson (C–R) estimate of 0.921 ('$M = 0.082$'). Using earplug laminae and the entire adult series (8 years and older), their *C–R* estimates were 0.909 for females and 0.922 for males.

Earplug laminae are the reference time scale for ovarian corpora; the relation is linear and significant (see above) but not remarkably so, with $r^2 = 0.614$. Both time scales are questionable but of interest, because only about one half of the earplugs were readable and because readings for older animals may not be accurate (Rice and Wolman, 1971).

To obtain variances to facilitate comparisons (not presented in Rice and Wolman, 1971), I have recalculated *C–R* survival rates from age-class frequencies for four cases: males and females separately, using laminae and all data; females using laminae but truncating 'older' (30 years and older) whales; and females using corpora (Table 6). Adult male survival (0.920, S.E. $= 0.012$, $n = 49$, not in Table 6) is significantly different from adult female survival ($Z^2 = 5.0$, $P < 0.01$). Since only female survival is of interest for the rate-of-increase calculations, the sexes were treated separately and males not considered further here.

Following Robson and Chapman (1961), a comparison of *C–R* and Heincke estimates at ages 8–12 showed no under-representation of those age classes ($Z^2 = 0.55$, 0.47, 0.38, 0.15, respectively; none significant at $\alpha = 0.05$). Consequently 8 years is a valid starting point for *C–R* computations.

Table 5

Age composition of gray whales from Rice and Wolman (1971) based upon ovarian corpora and earplug laminae as time scales

Estimated age (years)	Ovarian corpora		Ear-plug laminae		
	No. corpora	No. individuals	No. laminae	No. females	No. males
1			2	5	3
2			3	2	5
3			4	1	2
4			5	2	4
5			6	4	3
6			7		5
7			8	5	7
8	1	8	9	3	3
9			10	3	5
10	2	15	11	3	6
11			12	5	3
12	3	12	13	4	6
13			14	1	6
14	4	11	15	1	2
15			16	3	
16	5	9	17	2	4
17			18	1	3
18	6	11	19	3	3
19			20	5	3
20	7	11	21	1	6
21			22	1	4
22	8	6	23		2
23			24	4	1
24	9	8	25		1
25			26	1	
26	10	5	27	1	
27			28	2	1
28	11	3	29		2
29			30	2	
30	12	5			
31					
32	13	4	33		1
33					
34	14	2	35		1
35					
36	15	2			
37			38		1
39			40	1	4
40			41	1	
46	20	1	47		1
47			48	1	
50	22	1			
51					
57			58		1
69			70		1
76	35	1			
77					

Table 6

Estimates and standard errors of apparent adult female survival from frequency per age class using ear-plug laminae and ovarian corpora counts as age indicators, with and without truncation of age-30 and older individuals (original data from Rice and Wolman, 1971). A is the mean apparent survival rate and Z the corresponding apparent mortality coefficient

	Ageing technique	
Data	Ovarian corpora	Ear plug laminae
All 8+ years females	0.918 ± 0.007	0.910 ± 0.012
8–30-years females		0.908 ± 0.012
	$\bar{A} = 0.912$ ($Z = 0.092$)	

There is no well defined criterion with which to select one of the three available estimates of female survival as the best estimate (Table 6). All are quite close, however, and overlap in 95% confidence intervals. A simple average of the three was calculated: $\bar{A} = 0.912$ ($Z = 0.092$) where A is apparent survival (Z is total instantaneous mortality), including effects of population growth (G) and fishing mortality (F). The female data are fitted well by a geometric series with $A = 0.912$ ($X^2 = 34.27$, $d.f. = 29$, $P = 0.77$), validating the use of the C–R statistics.

Following Ohsumi (1976) I have estimated natural mortality (M) by subtracting population growth (G) and fishing mortality (F) from apparent total mortality (Z): $M = Z - (F + G)$. However, determining F and G during the time period of interest (about 40 years prior to 1967, since about 98% of the population was 40 or less in 1967 – Table 5) is at best a gross approximation.

Reported catches for 1927–1967 (summarized in Reilly, 1981) averaged only about 80/year, but they are reported to have increased to over 100/year during the 20 years immediately preceding 1967. There is no direct estimate of the population size or the precise nature of its changes during this period. An estimate does exist of $F + G$ for the 13 years following 1967. For lack of better information, I tentatively assumed $F + G$ constant at the same rate prior to 1967 as that measured for 1967–1980, or about 0.037. From $Z = -ln\ (0.912) = 0.092$ and from (1), M was approximated as $M = 0.092 - 0.037 = 0.055$ ($S = 0.946$).

Table 7

The ranges of pregnancy rate (P), juvenile survival (S_j), adult survival (S_a) and age at sexual maturation (X_m) determined here for two different population levels, with dominant eigenvalues (λ) for each set. S_j was adjusted to yield $\lambda = 1.037$ for *circa* 1967. For near zero,[2] P was adjusted to yield $\lambda = 1.09$, holding S_a, and X_m at near-zero[1] levels

Population level	P	X_m	S_j	S_a	λ
Near zero[2]	0.642	5	0.940	0.945	1.090
Near zero[1]	0.500	5	0.940	0.945	1.069
Circa 1967[3]	0.469	8	0.893	0.945	1.037

[1] For maximum P of 0.50.

[2] For maximum P of 0.642.

[3] Approximately 12,500.

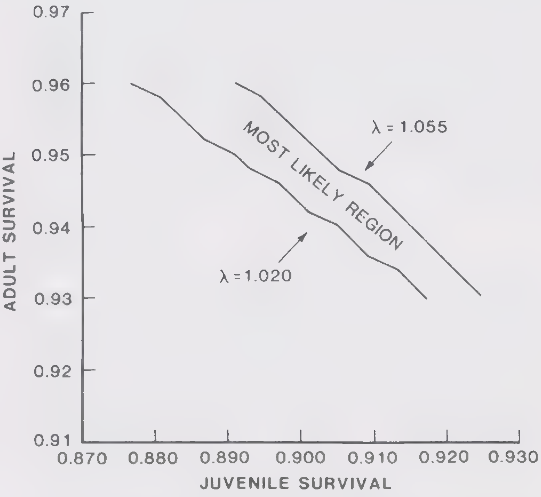

Fig. 5. Relationship between juvenile survival, adult survival and *per capita* rate of increase for the *circa*-1967 gray-whale population. A best estimate of 0.893 for juvenile survival corresponds to adult survival of 0.945 and $\lambda = 1.037$.

Juvenile survival rate

With other vital rates set at their presumed *circa*-1967 values ($P = 0.469$, $S_a = 0.946$, $X_m = 8$, $\lambda = 1.037$) juvenile survival S_j was estimated to be 0.893 (Table 7). This corresponds to a mortality coefficient of 0.113. Using the two-compartment model (1) and slightly different values for vital rates, Ohsumi (1976) estimated the juvenile mortality coefficient to be 0.167, notably higher than my estimate of 0.113. This latter estimate is hopefully more accurate, because (1) Ohsumi's (1976) estimate of pregnancy rate was probably too low; (2) his estimate of adult mortality rate was probably too high; and (3) population growth was not accounted for in his estimation procedures.[3]

The estimate of juvenile survival produced here is dependent on the accuracy of my estimates of other vital rates. In Fig. 5 the sensitivity of estimates of S_j to values of adult survival and rate of increase is examined. The figure shows a region defined by $S_a = 0.945 \pm 0.015$ and $\lambda = 1.037 \pm 0.018$. Within these boundaries juvenile survival varies from about 0.878 to about 0.924. The central value of this 'most likely region' is, by definition, 0.893.

Maximum rate of increase

The maximum rate of increase which could be achieved by gray whales is dependent on the extremes approached by other vital rates as density nears zero. For pregnancy rate, if a two-year minimum calving interval is assumed, the maximum rate will be 0.5. Given the range in observed ages at sexual maturation from 5 to 11 years, it seems reasonable to assume that the population median or mean age at sexual maturation would approach 5 years at minimum. Since adult survival (assumed density-independent here) was estimated to be 0.946, it is assumed that juvenile survival would approach but probably not equal or surpass this rate. Consequently a value of 0.940 was assumed for this exercise. Given this set of vital rates (Table 7) and a Leslie matrix constructed as in (2), a dominant eigenvalue of 1.069 was calculated. This equals a maximum rate of increase of approximately 6.7% per year for the California stock of gray whales, if a stable age structure can be assumed in populations at very low levels.

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[3] F was set at $0.0175 = 179/10{,}242$ from the average kill 1955–1966 (Zimushko and Ivashin, 1980) and from the average population size during those years as extrapolated from the exponential model estimated for the years covered by the Monterey census by Reilly *et al.* (1983).

Considering the uncertainty encountered here in defining maximum pregnancy rate, and the possible rate of increase of 8.8% per year implied by early Pt Loma censuses, it is of interest to determine what the pregnancy rate must be to result in an 8.8% rate of increase. Holding the other vital rates at their previous extremes, pregnancy rate must be 0.64 for $\lambda = 1.09$. It does not seem likely that the population pregnancy rate could exceed the ovulation rate, calculated at 0.518. However, sufficient information does not exist on maximum pregnancy rate to dismiss the higher P and λ values considered here.

CRITIQUE AND SUMMARY

This study reviewed all available information on realized rate of increase from four series of sighting censuses and on vital rates and related biological topics from two specimen series and a number of previous analyses. It then utilized information from both topics to estimate the maximum rate of increase that gray whales might achieve.

Although gray whales are perhaps the best studied of all baleen whales, much research is still needed to satisfactorily describe their life history and population dynamics. The length of gestation, verification of ageing, flexibility in ovulation and conception, and (ultimately) the minimum calving interval are among the major topics requiring further research. Estimates of juvenile survival and maximum rate of increase produced here are contingent on the validity of estimates and assumptions made regarding other aspects of the life history. Future findings from direct observation may indicate a reassessment of juvenile survival and maximum rate of increase. The following outline summarizes the information reviewed and (in some instances) the parameters re-estimated here.

Observed rates of increase

1. The Monterey shore censuses conducted annually from 1967–68 through 1979–80 indicate a net rate of increase of 2.5% per year. If the removals from the Soviet subsistence fishery are considered as well, the mean net productivity was approximately 3.7% per year.
2. Census series from Scripps in the late 1940s, Point Loma in the 1950s through 1970s and from the calving grounds are not reliable as indices of population change.

Vital rates

3. Life-history data for the estimation of vital rates are available from two sources: a series collected by Rice and Wolman (1971) off the central California coast, and a limited sample from the Soviet subsistence fishery. All available data appear to apply roughly to the 1967 population.
4. The mean age at sexual maturation was 8 years, with a range of ages from 5–11 years for both sexes.
5. The population pregnancy rate *circa* 1967 was estimated here to be 0.467 with a standard error of 0.045.
6. There is some uncertainty regarding the gestation period, but available data suggest a minimum period somewhat greater than 12 months.
7. The *circa*-1967 ovulation rate was 0.518/year (S.E. = 0.059).
8. Lactation appears to have been near 7 months in duration.
9. The minimum calving interval is probably near 2 years. A report of seven simultaneously pregnant and lactating females on the summer grounds needs further investigation.
10. Female adult survival rate was estimated to be 0.945, corresponding to a mortality coefficient of 0.056. Juvenile survival was estimated to be within the range 0.878–0.924, with a best estimate being 0.893, corresponding to a mortality coefficient of 0.113.
11. Adult male survival is significantly higher than adult female survival, as calculated using ear-plug laminae as indicators of age.

Maximum rate of increase

12. The asymptotic maximum or intrinsic rate of increase for the stock is estimated to approach 6.7% per year as population density approaches zero.

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ECHNIQUES AND APPROACHES

Early Life History Descriptions

E. M. Sandknop, B. Y. Sumida and H. G. Moser

ISHERIES studies require accurate identification of subject species. Identification of the developmental stages of fishes complicated by the small size of the specimens, their fragility, d the relatively great changes in their structure and pigmen- tion. Experience has shown that major changes can occur over ry small growth increments and these can only be documented a continuous growth series. Published descriptions of de- lopmental series vary in quality, perhaps more than do species scriptions of adults. Prior to Bertelsen (1951) and Ahlstrom d Ball (1954), most published descriptions were based on atively few specimens, which were described individually. In eir study of the early life history stages of the jack mackerel *rachurus symmetricus*), Ahlstrom and Ball (1954) used over 0 eggs and a series of about 250 larvae, transforming speci- ens, and juveniles to describe development. Changes in struc- re and pigmentation were thus described as a dynamic con- uum, with emphasis on variation, in contrast to the approach most previous workers. Developmental osteology was con- lered an integral part of the description as were seasonal and graphic distributions of eggs and larvae. This paper was fol- wed by several others (Ahlstrom and Counts, 1955, 1958; hida et al., 1958; Kramer, 1960) and these became models subsequent descriptive papers, including some which treated veral species in various taxonomic groups (Moser and Ahl- rom, 1970; Ahlstrom, 1974; Ahlstrom et al., 1976; Moser et 1977; Kendall, 1979; Brownell, 1979; Richardson and ashington, 1980; Fahay, 1983; Leis and Rennis, 1983). The lowing is a brief account of the elements involved in preparing rly life history accounts of teleosts.

Sources

The major source of material is plankton collections. Typical rvey tows strain a column of water 200 m to the surface and ample eggs and subsequent larval stages of a major portion of he fish fauna (Smith and Richardson, 1977). Fishes which have ighly stratified vertical distributions are undersampled by blique tows and require special gear or tow strategies. For xample, surface dwellers can be sampled by neuston nets (Zaitsev, 1970; Nellen and Hempel, 1970; Hempel and Weikert, 1972; Nellen, 1973a; Ahlstrom and Stevens, 1976) and those species residing near the bottom may be sampled by epi-benthic plankton nets (Schlotterbeck and Connally, 1982). Larger larvae and transforming stages are poorly sampled by typical survey tows principally because of accumulated mortality, increased avoidance capacity, and migration out of the sampling zone. These stages are more effectively sampled by trawls (Tranter, 1968), dip-netting with attractor lights (Klawe, 1960), light traps (Faber, 1982), and fish predators (Haedrich and Nielsen, 1966). Recently, scuba divers have collected oceanic larvae with their delicate structures intact (Harbison et al., 1978; Govoni et al., 1984). Developmental series may also be obtained by rearing larvae from eggs collected at sea or from captive brood stock (Houde et al., 1970, 1974; Houde and Swanson, 1975; Richards et al., 1974; Houde and Potthoff, 1976; Moser and Butler, 1981). This method becomes essential when working with speciose faunas (e.g., *Sebastes*, warm water shorefishes), if only to determine which species cannot be identified.

Use of Specimens

The characters and techniques used in identifying developmental stages are discussed elsewhere in this volume (see Kendall et al.; Matarese and Sandknop; Powles and Markle). From the continuous developmental series two subseries are assembled and these form the basis for the description. The first series is used to describe morphology and pigmentation. Specimens in the second series are cleared and stained by a variety of techniques to describe the development of cartilaginous and osseus features (Potthoff, this volume).

The number of specimens used to construct these series is dependent on several factors: 1) specimen availability, 2) length (duration) of the development period, and 3) complexity of developmental change. A guideline is that there should be enough specimens to demonstrate the beginning, progression and completion of significant developmental changes in morphology and pigmentation. Usually more specimens are required for species which have extended larval periods; however, many fishes which transform at small sizes undergo great change over small length intervals. For example, lined sole (*Achirus lineatus*) hatch at 1.6 mm, transform at about 4.0 mm, and complete a large suite of developmental changes over a 2.5 mm length interval (Houde et al., 1970). The majority of marine teleosts transform between 10 and 30 mm and, for these, major developmental events can be documented by specimen length increments of 0.5–1.0 mm. Multiple samples representing 1 mm-intervals are required to study fine-scale character variation; however, such studies have rarely been done (Ahlstrom and Moser, 1981).

A table of morphometric measurements constructed from the unstained series provides data on the size at important developmental milestones (e.g., hatching, notochord flexion, fin formation, transformation) and provides a basis for analyzing structural change and allometric growth. These specimens can be used to construct character matrices of complex or diagnostic pigment changes. Illustration specimens chosen from the series provide an integrated view of major characters and also, if accurately executed, are themselves morphometric and meristic documents (Sumida et al., this volume).

The stained series is used to construct a meristic table that forms the basis for following the development of fin rays and supporting elements, the axial skeleton and cranial bones (Dunn, this volume). Fine bony structures, such as cranial spines are also apparent in these preparations.

Published descriptions employing these basic elements are the basis for ontogenetic studies of fishes. These are essential for the identification of ichthyoplankton collections, and also present characters for systematic analysis. Data provided in these descriptions have proved useful in studies of the phys ology, behavior and ecology of the early stages of fishes.

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ESTIMACION DE LA BIOMASA DE LA POBLACION DESOVANTE DE ANCHOVETA PERUANA **Engraulis ringens** EN 1981 POR LA APLICACION DEL "METODO DE PRODUCCION DE HUEVOS"

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RESUMEN

Un nuevo método, "Método de Producción de Huevos", fue usado para estimar la biom sa desovante de la anchoveta peruana, **Engraulis ringens**. de las áreas norte y centr Este método se basa en el estimado conjunto de la producción de huevos por unidad peces adultos por unidad de tiempo. Se describe el método en detalle. Se obtuvieron l siguientes resultados:

1. Producción de huevos en el área investigada: 6.4963×10^{13} huevos
2. Fecundidad parcial: 15, 401 huevos/hembra.
3. Porcentaje de hembras desovantes/día: 16.04 %
4. Proporción sexual: 56.43 % de hembras.
5. Peso promedio de hembras 25.84 g.
6. Mortalidad diaria de huevos 65 %

La biomasa desovante del stock de anchoveta de las áreas norte y central en agosto - setiembre de 1981 fue de 1.2 millones de toneladas métricas con límites de confianza a 95 % de ± 56.80 %

ABSTRACT

A new method, the "Egg Production Method", was used to estimate the spawning biomass of the central and northern stock of Peruvian anchovy, **Engraulis ringens.** It is based on the joint estimation of the egg production per unit sea area and the egg production per unit adult fish per unit time. The method has been described in detail. The following results were obtained:

1. Daily egg production in the surveyed area: $6,4963 \times 10^{13}$ eggs
2. Batch fecundity: 15,401 eggs/female.
3. Percentage of females spawning/day: 16.04 %
4. Sex ratio 56.43 % females.
5. Average female weight: 25.84 g.
6. Daily egg mortality: 65 %

The spawning biomass of the central and northern anchovy stock in August/September 1981 was 1.2 million metric tons with 95 % confidence limits ± 56.80 %

INTRODUCCION

La biomasa de la enchoveta peruana, **Engraulis ringens**, ha sido estimada por métodos acústicos y análisis de población virtual. Reconociendo la necesidad de un estimado independiente de la biomasa de la población de anchoveta, el Instituto del Mar decidió en noviembre de 1980, aplicar el "Método de Producción de Huevos"(MPH) para estimar la biomasa del stock norte y central de la anchoveta peruana

El "Método de Producción de Huevos" es un nuevo método para el estimado absoluto, instantáneo y directo de la biomasa desovante. Se basa en el estimado conjunto de la producción de huevos por unidad de área de mar, por unidad de tiempo y producción de huevos por unidad de peces adultos por unidad de tiempo (Parker, 1980; Stauffer and Picquelle, 1980). Los parámetros del modelo (Parker, 1980) del "Método de Producción de Huevos" incluyen estimados de la producción diaria de huevos en el mar, fecundidad parcial, frecuencia de desove, proporción sexual y peso de hembras

El MPH ya ha sido exitosamente usado tres veces por el Southwest Fisheries Center, California, para estimar la biomasa desovante de la anchoveta del norte en 1980 (Stauffer and Picquelle, 1980); en 1981 (Staúffer and Picquelle, 1981) y 1982 (Picquelle and Hewitt, 1982). Las ventajas del MPH son (Stauffer and Picquelle, 1980)

1. Gran reducción de tiempo de barco y costos asociados requeridos;
2. Cada parámetro incluído en el modelo de biomasa se basa en una interpretación biológica y no es dependiente de los estimados históricos o índices de abundancia;
3. El nivel de precisión de cada parámetro y del estimado final de biomasa puede ser determinado;
4. Provee un estimado instantáneo de producción de huevos y de biomasa desovante.

El MPH se originó en el hallazgo de Hunter and Goldberg (1980) por el que los folículos post-ovulatorios, que son estructuras que permanecen en el ovario después que la hembra ha desovado, pueden ser usados para determinar el tiempo que ha transcurrido desde el último desove.

Usando ejemplares de anchoveta vivos en el laboratorio, que fueron indúcidos a desovar artificialmente (Leong, 1971), Hunter and Goldberg (1980) y Hunter and Macewicz (1980) han podido determinar la edad de los folículos post-ovulatorios.

La incidencia de los folículos post-ovulatorios de determinada edad es usada para determinar la frecuencia del desove. La fecundidad parcial es determinada por conteo del número de ovocitos hidratados (Hunter and Goldberg, 1980, Hunter and Macewicz, 1980).

El número de muestras de huevos requerido para obtener un estimado de precisión razonable fue determinado anteriormente en base a resultados de cruceros previos de IMARPE y EUREKAS entre los años 1965 y 1979 (Santander **et al.**, 1982). Los detalles técnicos del planeamiento del crucero son descritos en Smith **et al.** (1983)

El proyecto fue desarrollado por el Instituto del Mar en el marco del "Proyecto Cooperativo Peruano-Alemán de Investigación Pesquera" (PROCOPA), (que parcialmente es financiado por la Agencia Alemana, de Cooperación Técnica, GTZ) y el Southwest Fisheries Center.

A fines de 1980 se inició la preparación para llevar a cabo el estimado de biomasa durante la principal estación de desove de 1981. El crucero se realizó entre agosto y setiembre de 1981. Las muestras se procesaron hasta diciembre de 1981. Los resultados finales se presentaron en enero de 1982. Esta contribución presenta los resultados del estimado de la biomasa desovante de la anchoveta peruana y describe en detalle los métodos usados.

MÉTODOS

Durante el ciclo de desarrollo desde el ovocito sin vitelo en el ovario hasta ser depositado en el mar, el huevo pasa a través de una serie de diferentes estadíos. El método para el estimado de biomasa desovante de anchoveta (Parker, 1980) que aquí se describe, se basa en gran parte en la determinación de estos estadíos (Hunter and Goldberg, 1980) (Fig.1). El pequeño ovocito sin vitelo, con un diámetro menor de 0.2 mm. (1), crece en el ovario hasta alcanzar un diámetro de 0.5 a 0.7 mm, proveyéndose de vitelo (2). El ovocito es circundado por una capa folicular. De 10 a 15 horas aproximadamente antes del desove, el ovocito comienza a hidratarse.

El eje mayor del ovocito, el cual ahora ha adoptado la forma ovoidal típica del huevo de anchoveta se incrementa a 1.3 mm (3), con lo que el volumen total aumenta cuatro veces Hunter et al., (1984). Este proceso es llamado hidratación. Los ovarios con ovocitos hidratados son reconocibles fácilmente a la vista, porque la dilución del vitelo hace transparente a los ovocitos. Después del desove, el folículo, ahora llamado folículo post-ovulatorio (4), se pliega pero permanece en el ovario y degenera rápidamente en los 3 días siguientes. (Hunter and Goldberg, 1980).

Luego el huevo deja el folículo y el ovario y es depositado en el mar (5). Después de la fertilización en el mar, pasa por una serie contínua de diferentes estadíos (Fig.5) cuya duración es dependiente de la temperatura del mar donde se desarrolla.

I. Muestreo en el campo.

Se decidió estimar la biomasa desovante de la sub-población norte-central de la anchoveta, la cual se extiende de Pisco en el sur (14°00'S), a Punta Aguja en el norte (06°00'S) (Fig.2). Investigaciones previas de huevos y larvas (Santander y S. de Castillo, 1979), mostraron que la subpoblación del sur tiene su límite norte en la latitud 14°S. Como el rango de la subpoblación del sur se extiende en aguas chilenas, las que no podrían ser incluidas en este crucero y como la disponibilidad de tiempo del barco no fue suficiente para cubrir toda la costa peruana, el estimado de biomasa desovante se limitó a la subpoblación norte - central de la anchoveta.

1. Muestreo de la anchoveta adulta.

La anchoveta adulta fue pescada con "boliche" desde una bolichera, la "Loreto 5", la cual tiene una capacidad de 270 toneladas. El boliche tenía una profundidad de 70 m y una circunferencia de 800 m. Durante el crucero fue reemplazado por otro con una circunferencia de 700 m.

Siguiendo la metodología del estimado de biomasa de la anchoveta de California (Stauffer and Picquelle, 1980), se estimó que se requería un mínimo de 40 calas positivas para cubrir suficientemente la subpoblación norte-central. El crucero del 25 de agosto al 17 de setiembre se inició en el sur y prosiguió en dirección norte, de 5 a 10 días después del crucero de muestreo de huevos con el BIC Humboldt.

Debido a las condiciones adversas del clima y la escasez de cardúmenes de anchoveta lejos de la costa, el boliche fue generalmente usado dentro de las 20 millas de la costa y los cardúmenes de anchoveta fueron detectados con ecosonda. El número total de calas positivas para anchoveta fue de 49. La mayor parte de las muestras provienen del sur del área de investigación debido a las condiciones adversas del clima en el norte, lo que impidió el uso del boliche, (Fig.2). Todas las calas, excepto una, fueron hechas entre las 7.00 y las 23.00 horas (Tabla 4).

Una cala típica desde el lanzado de la red hasta su recuperación a bordo duró usualmente de 2 a 3 horas. Una vez en cubierta, se procedió a abrir los peces desde el ano hasta las aletas ventrales. Debido a la rápida degeneración de los folículos post-ovulatorios, solamente los ejemplares que llegaban vivos a bordo fueron seleccionados.

Los peces fueron preservados en solución de formaldehido al 4 % buferada, la que se preparó según Hunter, (1984).

La fórmula para la preparación de 10 litros de esta solución es la siguiente:

9 litros	agua destilada
1 litro	solución de formaldehido (40 %)
65 gramos	fosfato de sodio dibásico (granular Na_2HPO_4)
40 gramos	fosfato de sodio monobásico (granular $NaH_2PO_4.H_2O$).

Debido a que los ejemplares debían someterse a análisis histológicos, el uso de formaldehido mezclado con agua de mar tuvo que ser evitado porque causa un precipitado blanco. Si no se dispone de agua destilada se puede usar agua fresca. Para asegurar la preservación, solamente 5 ejemplares fueron colocados en cada recipiente de 1 litro.

El número de peces colectados por muestreo fue determinado de acuerdo a un esquema sugerido por Mac Call (Ms). El objetivo principal de este esquema fue obtener 25 hembras de cada cala. Con el fin de minimizar la subjetividad y maximizar la conveniencia y utilidad, MacCall propone el siguiente procedimiento:

a. Inmediatamente después que los peces están a bordo, dos personas seleccionan anchovetas al azar, les hacen una incisión y las colocan en recipientes.

b. Una persona llena 5 recipientes con peces no examinados (5 ejemplares por recipiente). Luego espera instrucciones de la otra.

c. La otra persona sexa 10 anchovetas y las coloca en dos recipientes. Cuenta el número de hembras y consulta la carta de decisión (Tabla 1a) sobre el procedimiento a seguir.

d. Ambas personas continúan preservando peces no examinados hasta que haya sido completado el número suficiente de recipientes.

Ejemplo:

Cada recipiente debe contener 5 ejemplares. Suponiendo que se encuentran 7 hembras entre los primeros 10 ejemplares sexados (Tabla 1a. columna 1), según la columna 2, tienen que ser sexados 10 ejemplares adicionales. Y si 5 ejemplares de éstos son hembras, dan un total de 12 ejemplares hembras (columna 1). Según la columna 3, 7 recipientes más tienen que ser llenados con peces. La Tabla 1b indica el número total de recipientes y el número total de peces que ellos contienen. En este ejemplo, después de examinar el segundo lote de 10 peces, se encontró un total de 12 hembras. Para la preservación de 20 peces originalmente sexados (dos lotes de 10 ejemplares), se necesitaron 4 recipientes. Se prepararon 7 recipientes adicionales (columna 2 Los 11 recipientes contenían un total de 55 ejemplares (Tabla 1b).

En las calas donde la proporción de ejemplares hembras es bajo, puede ocurrir que tienen que ser sexados varios cientos de peces hasta encontrar 25 ejemplares hembras, para lo cual se estableció la preparación de un límite arbitrario de 24 recipientes (o sexar 120 ejemplares). La base estadística para este procedimiento de muestreo [illegible] MacCall ([illegible]).

Estos peces fueron muestreados para análisis histológicos, con el fin de registrar la incidencia de folículos post-ovulatorios para la determinación de frecuencia del desove. Después que fue colectado el número señalado de peces, se hizo un intento de muestrear 25 hembras adicionales con visibles ovarios hidratados para la determinación de fecundidad. Sin embargo, como la hidratación se puede diferenciar al ojo solamente cuando está en estado muy avanzado, se chequearon solamente las calas después de 16.00 hrs. para ejemplares adicionales de hembras hidratadas.

2. Muestreo de huevos de anchoveta.

Santander *et al.* (1982) estudiaron la probalilidad de distribución de huevos de anchoveta, a partir del análisis estadístico de 4,000 muestras de ictioplancton, colectadas entre 1965 y 1979 en el área principal de desove de la anchoveta peruana.
Determinaron que eran necesarios alrededor de 1,000 muestras de ictioplancton en el área entre Punta Aguja y Pisco para obtener una precisión de 30% en el estimado de la producción de huevos en el mar. Este fue el objetivo del crucero de muestreo entre agosto y setiembre de 1981.

Los requisitos considerados en la planificación del crucero fueron:

1. La máxima cobertura latitudinal del área de desove, que incluye el área principal de desove de los últimos años, que se extiende de Punta Aguja a Pisco de 06°00' a 14°00'S (Santander, 1981).

2. La cobertura en distancia de la costa. Para cubrir el área de desove, se decidió abarcar hasta 90 millas de distancia de la costa, previendo una mayor expansión del desove de la anchoveta; así como cubrir además el área de desove de sardina (*Sardinops sagax*) para la planificación del muestreo de esta especie en 1982.

3. La colección vertical máxima en relación a la distribución del desove, que es de 70 metros a la super

ficie (Santander y S. de Castillo 1973).

4. La realización del crucero durante el pico del desove entre agosto y setiembre.

Los detalles técnicos del crucero son descritos en Smith et al. (1983). Las estaciones de muestreo fueron distribuidas en 53 perfiles perpendiculares a la costa (Fig. 3), 18 perfiles de 90 millas con aproximadamente 31 estaciones en cada uno y 35 perfiles de 30 millas con 11 estaciones por perfil. La distancia entre perfiles fue de 10 millas, y la distancia entre estaciones de muestreo fue de 3 millas.

El muestreador utilizado fue la red CalVET (CALCOFI vertical egg tow) diseñado por P.E. Smith, fundamentalmente para la aplicación del "Método de Producción de Huevos" (Fig.4). Las características de este muestreador son 25.23 cm de diámetro de boca, con un área de 0.05 m^2, y la malla es de 333μ. La medida de la malla esta seleccionada para la retención de los huevos de anchoveta (P.E. Smith, Ms).

El tamaño del muestreador, así como la forma de colección vertical, facilitan el manipuleo del equipo y reduce el volumen del agua filtrada en la columna muestreada, lo que facilita el procesamiento de la muestra en el laboratorio.

Se instaló un flujómetro tipo digital Modelo 2031 en la boca de la red para controlar la obstrucción de la malla, la que es detectada por cambios en las lecturas consecutivas.

Se usó un depresor cilíndrico de 36 kilogramos

La colección que se hace es en la columna vertical de 70 metros de profundidad a la superficie, en un minuto con una velocidad promedio de 1.17 m/seg. En una colección la red filtra 3.5 m^3 de agua (70 m x 0.05 m^2). Las muestras de huevos fueron colectadas durante el crucero BIC Humboldt, de Pisco a Punta Aguja del 21 de agosto al 13 de setiembre.

Se colectaron 925 muestras de ictioplancton con la red CalVET. En cada estación de muestreo se registró la temperatura en superficie y a 10 m de profundidad. Se tomaron muestras de agua con botellas Niskin a 10 m de profundidad para determinar la composición del fitoplancton.

Las muestras se preservaron con formalina al 5 % neutralizada, para lo que se procedió de la siguiente forma:

Se vació totalmente la muestra de la bolsa colectora, ayudándose con agua de mar (de una piceta) a un frasco de 500 cc. de capacidad a través de un embudo.

Se ocupa 3/4 del frasco aproximadamente con agua de mar, se agrega con una jeringa hipodérmica 25 cc de formalina concentrada (40 %) y 10 cc. de solución de borato de sodio. Se completa el frasco con agua de mar.

II. Procedimiento en el laboratorio.

1. Muestras de peces.

Para la determinación de la frecuencia del desove y la proporción sexual se requirieron por cada cala 20 hembras maduras y 800 g de peces respectivamente. Un mínimo de 25 hembras fueron submuestreadas de cada cala, para análisis histológicos, incluyendo a las hembras inmaduras. Los peces preservados de cada cala fueron procesados al azar hasta obtener los 2 mínimos requeridos (25 hembras y 800 g de peces). La longitud de cada pez fue medida con aproximación de 1 mm. y después de la remoción del exceso de fluído el peso total del cuerpo fue pesado con aproximación de 0.01 g. Se extrajeron los ovarios, se secaron con papel secante y se pesaron con aproximación de 0.001 g, luego fueron almacenados en la solución de formaldehido al 4 %, ya descrita anteriormente.

La fecundidad se determinó de acuerdo al método descrito por Hunter y Golderg (1980) y Hunter et al., (1984). En Hunter et al. (1984) se da una descripción detallada de la teoría fundamental, de las asunciones hechas y de los procedimientos usados. La forma más rápida y precisa para determinar la fecundidad de la anchoveta se realiza por medio de los ovarios hidratados.

Todos los ovocitos hidratados en el interior de un ovario son liberados pronto y el número reflejará el número total en la fecundidad parcial. Las ventajas de este método sobre los métodos tradicionales son:

a. Se ahorra tiempo, ya que los ovocitos necesitan solamente ser contados y no medidos, y

b. No surgen dudas sobre la disgregación de los modos en los diagramas de frecuencia - tamaño de los ovocitos, debido a la diferencia de tamaños de los ovocitos hídratados.

Las desventajas son

a. Las hembras con ovarios evidentemente hidratados que no han comenzado aún a desovar son encontradas solamente en la tarde o al anochecer; y,

b. Según la frecuencia de desove prevaleciente, un gran número de peces tienen que ser examinados hasta encontrar el suficiente número de hembras hidratadas.

Después de la preservación en solución formaldehida, los ovarios hidratados se caracterizan por su enorme tamaño, su transparencia y su consistencia blanda.

El examen histológico prueba el estado de hidratación. Todos los ovarios que van a usarse en el estimado de fecundidad deben ser chequeados para descartar los que presentan folículos post-ovulatorios, ya que su presencia indicaría que el desove ya ha tenido lugar, en cuyo caso la fecundidad parcial sería sub-estimada. Por lo que los ovarios hidratados con folículos post-ovulatorios tienen que ser eliminados de los estimados de fecundidad.

El procedimiento técnico se inicia con la absorción de líquido superficial del ovario con papel filtro. Para evitar el recuento del total de los ovocitos hidratados en un ovario, éste es submuestreado. De la mitad más grande del ovario, se toman tres segmentos de tejido. uno del centro y dos de la parte media, entre el centro y los extremos del eje mayor del ovario. Por conveniencia el peso de estas 3 sub-muestras debería ser aproximadamente de 30 a 50 mg para asegurar una cantidad entre 100 a 200 ovocitos hidratados por sub-muestra.

Las sub-muestras son pesadas con aproximación de 0.1 mg; luego son colocadas en una lámina porta-objeto y cubiertas con unas gotas de glicerina para ser contadas bajo el microscopio, usando 10 aumentos. Son fácilmente diferenciables de otros ovocitos por su gran transparencia y mayor tamano.

Además su superficie es arrugada debido a la preservación en formaldehido. Los ovocitos no hidratados son opacos y tienen una superficie lisa. El número promedio de los ovocitos hidratados de las tres sub-muestras está destinado a estimar el número total de ovocitos hidratados del ovario (fecundidad parcial), según:

$$F = \bar{n} . W_0 \qquad (1)$$

Donde:

F = Fecundidad parcial (número total de ovocitos hidratados en un ovario)

W_0 = Peso húmedo del ovario en g

$\bar{n}$ = Número promedio de ovocitos hidratados por gramo de sub-muestra

Hunter y Goldberg (1980) desarrollaron criterios para clasificar por edad los folículos post-ovulatorios en degeneración usando análisis histológicos. Esto permite la determinación del día en el cual la hembra desovó, y el cálculo de la frecuencia del desove de la población de anchoveta. Como los folículos post-ovulatorios degeneran rápidamente, su edad puede ser determinada solamente hasta 50 horas después del desove.

Métodos estándar son usados para el procesamiento histológico de los ovarios. Un pequeño cubo de alrededor de 0.5 mm de arista es cortado del centro del ovario, deshidratado en una serie de alcoholes y embebido en Paraplast. Los cortes histológicos fueron de 6μ y se tiñeron usando la técnica de hematoxylina-eosina.

La descripción detallada del método usado es dada en Alarcón (en prepa-

Los criterios para clasificar por edad los folículos post-ovulatorios se basan en los diferentes estadíos de degeneración por los que ellos atraviesan (Hunter and Goldberg, 1980).

La siguiente descripción es tomada de su publicación. Los nuevos folículos post-ovulatorios, de 0 - 6 horas después del desove, presentan estructuras de forma irregular compuestas de células foliculares columnares y un tejido conectivo subyacente (theca); 24 horas después la degeneración es pronunciada. Los folículos post-ovulatorios están bastante contraídos y las paredes de las células foliculares no se distinguen mayormente. El tejido conectivo subyacente (theca) no está muy diferenciado. 48 horas después del desove, la degeneración ha progresado más aún, los folículos se han reducido de 1/2 a 1/4 más pequeños que a las 24 horas, y el lumen es pequeño o indiferenciable.

Los folículos post-ovulatorios con más de 50 hrs después del desove son difíciles de clasificar por edad porque pueden ser confundidos con ovocitos atrécicos, los cuales son sometidos a un proceso de absorción. Hunter and Goldberg (1980) definieron cinco clases de ovarios:

Hidratados

Son los ovarios con muchos ovocitos hidratados. Los primeros estadíos de hidratación se caracterizan por la desaparición de la membrana nuclear, elementos nucleares esparcidos, situados en un polo del ovocito y con fusión sólo parcial de los glóbulos del vitelo en unos cuerpos grandes como placas (Hunter and Macewicz, 1980).

En los últimos estadíos, los ovocitos se agrandan por la entrada de fluído y el desove se considera inminente. Los folículos post-ovulatorios no están presentes.

Edad: día-0

Los nuevos folículos post-ovulatorios no muestran signos de degeneración. Los ovocitos hidratados pueden estar presentes ocasionalmente. Después del desove han transcurrido menos de 24 horas.

Edad: día-1

Los folículos post-ovulatorios muestran la degeneracion tal como la descrita para 24 horas después del desove. El tiempo transcurrido desde el desove es de más de 24 horas y menos de 48 horas.

(Maduros) no desovantes

Son los ovarios con muchos ovocitos vitelados. Ellos pueden contener folículos post-ovulatorios en estadío avanzado de degeneración, los cuales no pueden ser fácilmente diferenciados de las estructuras atrécicas. Con más de 48 horas desde el desove

Inmaduro

Con pocos o ningún ovocito vitelado.

Es importante anotar que por razones de conveniencia en las descripciones siguientes, los términos "edad : día - 1" y "edad : día - 2" serán usados en lugar de "edad : día - 0" y "edad : día - 1" de Hunter and Goldberg (1980)

2. Muestras de huevos.

El análisis de las muestras de ictioplancton consistió en la separación de todos los huevos y larvas de peces, e indentificación de huevos y larvas de anchoveta y sardina, los que fueron preservados separadamente. Para estudios futuros, también se separaron las larvas de "merluza" (**Merluccius gayi peruanus**), "jurel" (**Trachurus murphyi**) y "caballa" (**Scomber japonicus**) Los huevos de anchoveta se clasificaron en 11 estadíos según el progreso del desarrollo embrionario, determinado de las características anatómicas de los huevos (Fig. 5) (Santander y S. de Castillo 1973) Una descripción de los 11 estadíos se presenta en el Apéndice 1. Los huevos que no podrían ser asignados a ninguno de los 11 estadíos debido a que estaban opacos o sus estructuras internas estaban dañados, fueron clasificados como huevos "DIS" (desintegrados).

III. Análisis de datos

1. Parámetros de adultos

$\bar{\bar{W}}$. Peso promedio de hembras maduras.

De cada cala, las primeras 20 hembras maduras procesadas fueron utilizadas para la determinación del peso promedio del cuerpo. Se determinó el peso promedio para cada cala, $\bar{W}_i$. Se estimó el promedio y la varianza de acuerdo a:

$$\bar{\bar{W}} = \frac{\sum \bar{W}_i}{n} \qquad (2)$$

$$V_{(\bar{\bar{W}})} = \frac{\sum (\bar{W}_i - \bar{\bar{W}})^2}{n\,(n-1)} \qquad (3)$$

Donde:

$\bar{W}_i$ = Peso promedio del cuerpo de hembras maduras en la cala i.

$\bar{\bar{W}}$ = Peso promedio del cuerpo de hembras maduras en todas las calas.

n = Número de calas.

Stauffer and Picquelle (1980) corrigieron para los diferentes tamaños de muestras, cuando el número de hembras maduras por cala en la investigación de California era frecuentemente menor que 20. Para conocer el procedimiento de obtención del peso de arrastres de diferentes tamaños de muestra, ver Stauffer and Picquelle (1980).

El peso total del cuerpo de hembras hidratadas tuvo que ser ajustado en forma decreciente de acuerdo al incremento temporal del peso por la hidratación del ovario. Este ajuste se aplicó en todas las hembras cuyas secciones histológicas mostraban ovocitos hidratados, u ovocitos con el núcleo emigrado hacia el polo. El ajuste del peso total del cuerpo (W_i) fue determinado de la relación lineal entre el peso total del cuerpo (W_i) y el peso del cuerpo sin gonada (W_i^*).

$$W_i = -.3008 + 1.0639\,W_i^* \qquad (4)$$

$$n = 238$$

$$r = .9945$$

Esta regresión fue derivada usando 5 hembras maduras de cada cala, las cuales fueron clasificadas histológicamente como no hidratadas (Tabla 2).

E. Fecundidad parcial por hembra madura.

La fecundidad parcial se determinó utilizando 107 hembras, las que se colectaron en toda el área de muestreo (Tabla 3). Su peso fluctuó entre 13 y 40 g (peso sin gonada). Se encontró que la fecundidad parcial se incrementa exponencialmente con el peso de hembras sin gonada. Se derivó la siguiente regresión media geométrica (Ricker, 1973).

$$\ln E = 3.7637 + 1.7913 \ln W^* \qquad n = 107 \qquad (5)$$

$$\tfrac{1}{2}\, s^2_{yx} = 0.0233 \qquad r^2 = .7226$$

Donde:

E = Fecundidad parcial (Número de ovocitos hidratados).

W* = Peso del cuerpo de hembras sin gonada

Las 20 hembras maduras de cada cala que se procesaron inicialmente fueron seleccionadas con el fin de estimar su fecundidad por medio del modelo de regresión.

El promedio y la varianza se determinó de la siguiente manera:

$$\bar{\bar{E}} = \frac{\sum \bar{E}_i}{n} \qquad (6)$$

$$V_{(\bar{\bar{E}})} = \frac{\sum (\bar{E}_i - \bar{\bar{E}})^2}{n\,(n-1)} \qquad (7)$$

Donde:

$\bar{E}_i$ = Promedio de fecundidad parcial de las hembras maduras en la cala i.

$\bar{\bar{E}}$ = Promedio de fecundidad parcial de las hembras en todas las calas.

n = Número de calas.

R. · Fracción de hembras en la subpoblación.

La fracción de hembras (proporción sexual) fue estimada para cada cala, de una submuestra compuesta de los primeros 800 g. de peces. Se utilizó el peso total del cuerpo debido a que el peso sin gonada de machos no había sido determinado. El peso total del cuerpo de hembras hidratadas fue ajustado en forma decreciente según la ecuación (4). Los ejemplares inmaduros fueron incluídos debido a que no fue posible distinguir entre ejemplares machos maduros e inmaduros. Para obtener exactamente 800 g de peces fue necesario usar solamente la fracción del peso del último ejemplar en la cala que completó los 800 g. El promedio de la muestra y la varianza fueron estimados según:

$$\bar{\bar{R}} = \frac{\sum \bar{R}_i}{n} \qquad (8)$$

$$V_{(\bar{\bar{R}})} = \frac{\sum (\bar{R}_i - \bar{\bar{R}})^2}{n(n-1)} \qquad (9)$$

Donde

$\bar{R}_i$ = Fracción de hembras por peso en porcentaje en la cala i

$\bar{\bar{R}}$ = Fracción promedio de hembras por peso en porcentaje de todas las calas.

F. Fracción de hembras maduras desovantes por día.

Para la determinación de este parámetro fueron usados solamente los ovarios con folículos post-ovulatorios, los cuales fueron colectados en las muestras por lo menos 9 horas después del pico de desove (22.00) con el objeto de prevenir cualquier sesgo que pudiera surgir del muestreo de hembras durante la hora del día cuando estaban desovando. Las 49 calas positivas fueron distribuídas en un ciclo completo de 24 horas y la edad de los folículos post-ovulatorios podía ser determinada hasta 50 horas después del desove. En consecuencia podían ser separados dos grupos independientes de folículos post-ovulatorios de 24 horas: los del día-1, edad entre 9 y 32 horas, y los del día-2 con edad entre 33 y 56 horas. Debido a su independencia, estos dos grupos podían unirse, y el número de nuestras sería doblado a 98 (Alheit et al. 1984)

Suponiendo que el muestreo de hembras hidratadas o de hembras de edad de día-1 ó de día-2 no es sesgado, entonces la fracción de hembras desovantes para la cala i es estimada por:

$$F_i = \frac{m_{hi}}{m_i} \text{ o } \frac{m_{1i}}{m_i} \text{ o } \frac{m_{2i}}{m_i} \qquad (10)$$

Donde

$$m_{hi} + m_{1i} + m_{2i} + m_{ai}$$

Donde:

m_{hi} = Número de hembras hidratadas en la cala i

m_{1i} = Número de hembras con folículos post-ovulatorios de 9 a 32 horas de edad en la cala i.

m_{2i} = Número de hembras con folículos post-ovulatorios de 33 a 56 horas de edad en la cala i.

m_{ai} = Número de hembras que no están hidratadas y que no han desovado en las 9 a 56 horas anteriores (incluyendo hembras con folículos post-ovulatorios con una edad menor de 9 horas).

m_i = Número de hembras maduras en la cala i.

F_i = Fracción desovante en la cala i.

Los resultados mostraron que las hembras hidratadas estuvieron sobremuestreadas. Para corregir este sobremuestreo y bajo la asunción de que la verdadera fracción de las hembras hidratadas es la misma que la fracción de las hembras del día-1 ó día-2, m_{hi} es reemplazado por $\frac{m_{1i} + m_{2i}}{2}$

de tal forma que:

$$\hat{F}_i = \frac{m_{1i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}} \quad \text{ó} \quad (11)$$

$$\frac{m_{2i}}{\frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}}$$

Donde:

$\hat{F}_i$ = Fracción corregida de hembras con folículos post-ovulatorios de 9 a 32 horas de edad (hembras del día-1) ó 33 a 56 horas de edad (hembras del día-2) en la cala i.

Los estimados para promedio y varianza son dados por:

$$\bar{F} = \frac{\sum (m_{1i} + m_{2i})}{2 \sum \frac{(m_{1i} + m_{2i})}{2} + m_{1i} + m_{2i} + m_{ai}} \quad (12)$$

$$= \frac{\sum (m_{1i} + m_{2i})}{2 \sum m_{yi}}$$

$$V_{(\bar{F})} = \frac{1}{n\,(n - 1)} \sum \left(\frac{m_{yi}}{\bar{m}}\right)^2 (\hat{F}_i - \bar{F})^2 \quad (13)$$

Donde:

$\bar{F}$ = Fracción promedio de hembras desovantes por día de todas las calas.

m_{yi} = Número corregido de hembras maduras en cala i.

$$= \frac{m_{1i} + m_{2i}}{2} + m_{1i} + m_{2i} + m_{ai}$$

$\bar{m}$ = Número promedio corregido de hembras maduras.

$$= \frac{\sum m_{yi}}{n}$$

n = Número de muestras

2. Producción diaria de huevos en el mar.

La producción diaria de huevos en el área investigada, P, y su varianza pueden ser estimadas a partir de una regresión no lineal ajustada del modelo exponencial (Stauffer and Picquelle, 1981).

$$P_i = P_o\, e^{-Zt_i}\, \frac{1 - e^{-0.5Z}}{0.5Z} \quad (14)$$

Donde:

P_i = Número de huevos de edad t_i muestreado durante el intervalo de tiempo $(t_i, t_i + 1)$ ajustado a 0.5 de día (12 horas de intervalo) en el área investigada.

$$t_i' = t_i - \frac{t_1 + t_o}{2}$$

= Tiempo transcurrido (o edad) entre el desove y el inicio del intervalo de 12 horas

Z = Tasa diaria de mortalidad instantánea de huevos.

P_o es derivado como el intercepto del modelo de mortalidad exponencial. El modelo asume que (1) todos los huevos son desovados y fertilizados cada día al tiempo $\frac{t_1 + t_0}{2}$, (2) los huevos tienen una tasa constante de mortalidad instantánea positiva, y (3) la intensidad del muestreo es uniforme durante cada intervalo de 12 horas (Stauffer and Picquelle, 1981).

P_o es derivado del promedio de número de huevos (P_i) en el intervalo de 12 horas. A continuación se describe el cálculo de los valores t_i' y P_i.

Cálculo de t_i':

El período de desove diario ocurre de las 18:00 horas (t_o) a las 02:00 horas (t_1 = inicio de intervalo de las primeras 12 horas de muestreo) (Fig. 6).

Sin embargo, el modelo de mortalidad exponencial asume que todos los huevos son desovados en el tiempo $\frac{t_1 + t_0}{2}$ = 22.00 horas. El período de desove es seguido por los intervalos de muestras de 12 horas (t_i, t_{i+1}) Los valores para t_i y t_i' son dados en la Tabla 5.

Cálculo de P_i

Los intervalos de muestras de 12 horas (t_i, $t_i + 1$) son denominados categoría de edad. Los huevos son agrupados en estas categorías de edad según el esquema de la Fig. 7. El intervalo de desove "S" se asume que sea el intervalo de 8 horas de 18.00 a 02.00, con el tiempo nominal "0" en el punto medio a las 22.00 horas Los huevos con menos de 8 horas de edad colectados entre 18.00 y 02.00 no son incluídos en los estimados debido a que el desove no se ha completado durante este intervalo. Estos huevos son asignados a la categoría de edad "S" (Fig. 7). Los huevos de edades de 0 a 20 horas colectados entre 02.00 y 14.00 horas son asignados a la categoría de edad A_1. Los huevos de edades de 12 a 32 horas colectados entre 14.00 y 02.00 horas se asignan a la categoría A_2. Edades y categorías de edad sucesivas se asignan a los huevos con mayor desarrollo hasta que la eclosión se haga apreciable (> 5 % ,56 horas a 16.5°C).

Los huevos desintegrados ("Dis") se dividen en 2 grupos "Dis_1" y "Dis_2", de acuerdo a la hora de colección entre 02.00 y 14.00 horas y de 14.00 a 02.00 horas respectivamente.

Zweifel and Smith (Ms) desarrollaron un sistema gráfico para determinar la edad de los huevos de anchoveta y les asignaron las categorías de edad (S, A_1, A_2, etc.) por medio de: (1) el desarrollo embrionario, (2) temperatura del mar a 10 m de profundidad en la estación de la colección y (3) hora de la colección (Fig.8). Se usó el siguiente procedimiento:

Se clasificaron hasta 200 huevos de cada muestra por estadío de desarrollo (asignando 11 estadíos de desarrollo embrionario). Se da un ejemplo en la Tabla 6. Se encontraron huevos de los estadíos: II, III, V, VI, VII, IX, X, XI, Dis. Para asignarles las categorías de edad de las curvas de los estadíos de la Fig. 8, tiene que encontrarse el punto donde ellos cortan la temperatura del mar respectiva (eje de la Y) en la estación de la colección. Desde este punto se traza una línea recta hacia el eje de la X (hora del día) para encontrar la hora más próxima de colección de la muestra, sobre el eje de la X, hacia la derecha o hacia la izquierda. A los huevos bajo investigación se les asignó la categoría de edad (S, A, B, C) en la que es encontrada la hora más próxima de colección de la muestra.

Ejemplo. En el caso del estadío V, de la Tabla 6, los huevos fueron colectados a las 11.05 horas y la temperatura del mar a 10 m fue de 15.8°C. Siguiendo la curva del estadío V se encuentra el punto donde corta la temperatura 15.8°C del eje de la Y. Desde este punto se traza una recta al eje de la X, la que corta este eje a las 04.45 horas. Este punto (04.45 horas) está más próximo a la hora de colección de la muestra(11:05) hacia el lado derecho, que hacia la 11:05 del lado izquierdo. Por lo que se usa la del lado derecho. Esta hora 11.05, del lado derecho, cae en la categoría de edad B. Como la muestra fue colectada entre las 02.00 y las 14.00 horas (11.05) debe ser considerado en la categoría B_1 (Figura 7). En las muestras, donde se clasificaron solamente 200 huevos, el número de huevos en cada categoría es ponderado de acuerdo al número total de huevos de la muestra.

El área investigada fue dividida en 9 regiones. Solamente en 4 de ellas se encontraron huevos de anchoveta: 11, 21, 31, 22 (Fig.3, Tabla 7). El número de unidades de muestreo (red CalVET: $0.05 m^2$) de cada región se presenta en la Tabla 7. Las millas cuadradas son el producto de las dimensiones lineales, a lo largo de la costa, por la distancia de la costa del área respectiva. El área en millas cuadradas es multiplicada por el cuadrado del número de metros en una milla (1 milla = 1852 metros, 1 mn^2 = 3.430 x 10^6 m^2). Como la red Cal VET es 1/20 de m^2 ($0.05 m^2$) hay 6.860 x 10^7 unidades de muestreo en una milla náutica cuadrada. Por lo que en el caso de la región 11, hay

3.8484×10^{11} unidades de muestreo en el área de 5610 mn^2 (Tabla 7). El número total de huevos en cada categoria de edad y en las dos categorias "Dis" fue calculado en la siguiente forma. (Tabla 8). El numero total de huevos en cada región (Tabla 8, columna 4) fue dividido por el número total de estaciones (columna 3) para conseguir el número promedio de huevos por estación en la columna 5 (es decir por unidad de muestreo = 0.05 m^2). Este valor fue multiplicado por el número total de unidades de muestreo en cada región (columna 6) derivado de la Tabla 7 para obtener el número total de huevos por región (columna 7). Estos valores fueron sumados para cada categoría de edad para obtener el número de huevos de cada categoría de edad (columna 8) Luego los huevos "Dis" deben ser agrupados en categorías de edad según los siguientes procedimientos (Tabla 9). El número de huevos de la categoría de edad A_1, B_1 y C_1, los que fueron colectados entre 02.00 y 14.00 horas, fueron sumados y el porcentaje para cada categoría de edad calculado (Tabla 9, columna 3). Todos los huevos "Dis_1" (Tabla 8) colectados entre 02.00 y 14.00 horas, también fueron distribuídos entre las categorías A_1, B_1 y C_1, según los porcentajes de la columna 3 (columna 4). Los valores de las columnas 2 y 4 fueron agregados para dar el número total de huevos para cada categoría de edad (columna 5). El mismo procedimiento fue seguido para los huevos "Dis_2". En este caso debían ser incluídos los huevos de la categoría de edad "S" que fueron colectados entre las 14.00 y 02.00 horas.

La primera estación de cada perfil estuvo ubicada a 7 millas de la costa. Sin embargo, los análisis de muestras denotaron que habían algunos huevos más próximos a la costa y que podían no ser considerados. El número de estos huevos próximos a la costa se estimó en base a la abundancia de huevos de aquellas estaciones que estuvieron localizados a 12, 9 y 6 millas de distancia de la costa. Se asumió que la tasa de decrecimiento de la abundancia de 12 a 3 millas fue la misma que la tasa de 12 a 6 millas. No se da una descripción detallada de este procedimiento porque no forma parte del "Método de Producción de Huevos". Sin embargo, se debe enfatizar que se pueden evitar estas complicaciones, cubriendo el área de desove total cuando se muestrean los huevos. El número total de los huevos "próximos a la costa" fue 9.9956×10^{12}. Estos fueron distribuídos proporcionalmente en 7 categorías de edad (Tabla 10, columna 1 - 4). El número final de huevos en cada categoría de edad, P_i (columna 5), fue obtenida por compilación de los números de huevos de la columna 2 y 4.

Cálculo de P_o:

Solamente 4 de los 7 valores de P_i pueden ser considerados estimados no sesgados de la población de huevos de las edades establecidas. Los huevos en categoría de edad "S" son obtenidos de las muestras colectadas durante el desove. Por esta razón el número de huevos "S" es usualmente un subestimado del número de huevos con menos de 8 horas de edad. A las temperaturas encontradas durante la exploración en agosto/setiembre de 1981, es probable que en los huevos "C_1" y "C_2" de tres días de edad ya se hubiera producido alguna eclosión, y debido a ésto, los valores estarían también subestimados.

Por consiguiente 4 valores P_i (A_1, A_2, B_1 y B_2) son considerados en la regresión (Ecuación 14) para estimar el número de huevos, P_o, en el tiempo $\frac{t_1 + t_o}{2}$ (= 22.00 horas), el punto medio del período de desove de 18.00 a 02.00 horas (Fig.6). Los valores de P_i y sus respectivos valores de t_i' son dados en la Tabla 11. P_o y Z pueden ser estimados iterativamente por una regresión no lineal ajustada al modelo de mortalidad (ecuación 14). U. Damm preparó un programa de computación para aplicar esta regresión (Anexo II). Z tiene que ser dado incialmente, como un estimado razonable; derivado de la literatura.

3. Estimado de la biomasa desovante.

La biomasa desovante fue estimada

según el modelo desarrollado por Parker (1980) y modificado por Stauffer and Picquelle (1980)

$$B = K \frac{P_O \cdot W}{R \cdot F \cdot E} \qquad (15)$$

Donde:

- B = Biomasa desovante en toneladas métricas.
- P_O = Producción de huevos diaria en el mar, en el área explorada.
- W = Peso promedio de hembras maduras (g)
- R = Fracción de hembras en la población (Proproción sexual).
- F = Fracción de hembras desovantes maduras por día.
- E = Fecundidad parcial por hembra madura, en huevos por hembra.
- K = Factor de conversión, de gramos a toneladas métricas (= 10^{-6})

La varianza de la proporción de huevos del estimado de la biomasa desovante puede ser calculada aproximadamente por el método delta (Stauffer and Picquelle, 1980). La varianza del estimado de la biomasa es una funcion de la varianza y covarianza de los parámetros.

$$V_{(B)} \approx (K \frac{P_O W}{R.F.E})^2 (\frac{V(P_O)}{P_O^2}) + \frac{V(W)}{W^2} +$$

$$\frac{V(R)}{R^2} + \frac{V(E)}{E^2} + \frac{V(F)}{F^2}$$

$$+ \frac{Cov\ (P_O,\ W)}{P_O \cdot W} - \frac{Cov\ (P_O,\ R)}{P_O \cdot R} -$$

$$\frac{Cov\ (P_O \cdot E)}{P_O \cdot E} - \frac{Cov\ (R \cdot F)}{P_O \cdot F} -$$

$$\frac{Cov(W \cdot R)}{W \cdot R} - \frac{Cov(W \cdot E)}{W \cdot E} -$$

$$\frac{Cov\ (W \cdot F)}{W \cdot F} + \frac{Cov\ (R.E)}{R\ .\ E} +$$

$$\frac{Cov\ (R \cdot F)}{R \cdot F} + \frac{Cov\ (F \cdot E)}{F \cdot E}$$

RESULTADOS

Todos los datos originales serán dados en un informe de datos, el que será publicado separadamente.

Peso promedio de hembras maduras.

Hunter (1984) reportó que la preservación en formalina causa un incremento en el peso húmedo del cuerpo del 4 % . Por lo que se ha sustraído el 4o/o del peso promedio de cuerpo obtenido de cada colección. El peso promedio de cuerpo de hembras de 49 colecciones varió de 12.29 g. a 36.78 g. (Tabla 4). El peso promedio de cuerpo de hembras del área investigada fue de 25.84 g. con una varianza de 0.4494, una desviación estándar de 0.6704 y un coeficiente de variación de 0.0259 (Tabla 14).

Fecundidad parcial por hembra madura.

La fecundidad parcial promedio en las 49 colecciones varió de 4,154 a 27,408 huevos por hembra (Tabla 4). La fecundidad parcial promedio de todo el área investigada fue de 15,401 huevos por hembra con una varianza de 432,092.9182, una desviación estándar de 657.2898 y un coeficiente de variación de 0.0427 (Tabla 14). Un recuento más detallado de la fecundidad parcial de la anchoveta peruana es dada en Alheit et al.,(1983).

Fraccion de hembras en la subpoblación.

La proporción sexual de las 49 colecciones mostró grandes variaciones que van desde 12.62 a 90.50 % hembras (Tabla 4). Variabilidad similar en proporción sexual ha sido reportada por Klingbeil (1978), Hunter and Goldberg (1980) y Stauffer and Piquelle (1980). Hunter and Goldberg (1980) demostraron que la proporción sexual promedio (porcentaje de hembras) sobre una base de peso de la anchoveta peruana fue de 56.43 % con una varianza de 0.0007, una desviación estándar de 0.0259 y un coeficiente de variación de 0.0459 (Tabla 14).

Fracción de hembras maduras desovantes por día.

Teóricamente se pueden obtener tres estimados independientes de este parámetro: 1) Porcentaje de hembras con ovocitos hidratados, 2) Porcentaje de hembras con folículos post-ovulatorios del día-1, y 3) Porcentaje de hembras con folículos post-ovulatorios del día-2. Como las hembras con ovocitos hidratados tienden a ser sobremuestreadas (Stauffer and Picquelle, 1980; Alheit et al., 1984) no deben ser usadas en este análisis. Por otro lado, la edad de los folículos post-ovulatorios puede ser determinada solamente hasta alrededor de 50 horas después del desove. Los folículos post-ovulatorios de mayor tiempo pueden ser confundidos fácilmente con otras estructuras, tales como folículos atrécicos (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980).

Como se usó una red de arrastre para el muestreo de la anchoveta de California y porque las muestras sólo se obtenían de noche, Hunter and Goldberg (1980), Hunter and Macewicz (1980) y Stauffer and Picquelle (1980) podían usar solamente folículos post-ovulatorios de día-1 para la determinación de la fracción desovante. El uso de boliche para el muestreo de la anchoveta peruana permitió la colección de muestras en cualquier hora del día. Por lo que se obtuvieron 2 conjuntos de datos independientes para la determinación de la frecuencia del desove, hembras de día-1 y hembras de día-2. La forma de obtención de estas dos series de datos se muestra en la Tabla 12. El pico del desove se ha fijado a las 22.00 horas. Como la muestra colectada mas temprano fue a las 07.00 horas, esta hora ha sido considerada como el inicio del período del día-1 y del día-2, respectivamente. Los folículos post-ovulatorios encontrados a esta hora, según su estructura, fueron asignados a uno de los tres grupos siguientes: folículos post-ovulatorios del día-1, del día-2 o de mayor edad. A los que se les dieron edades de 9 a 32, 33 a 55 [illegible] de [illegible]5 horas respectivamente. La Tabla 13 [illegible] resumen de todos los datos: (1) número [illegible] (2) hora de colección, (3) número [illegible] hidratadas del día-1 (4) y día-2 (5) [illegible] número de horas posterior al desove de cada colección, (7) los valores corregidos de hembras hidratadas sobremuestreadas, (8) porcentaje de hembras hidratadas, (9) de hembras del día-1 y (10) del día [illegible] colección. El número de hembras [illegible] por colección (no ajustado) varía de 0 a 95 %, número de hembras del día-1 de 0 a 39.13 % y número de hembras del día-2 de 0 a 40.00 %. Como fue demostrado que el conjunto de datos de hembras del día-1, y de hembras del día-2 fueron independientes entre sí (Alheit et al. 1984), los dos conjuntos de datos fueron combinados. El conjunto de datos combinados da una fracción de desove de 0.1604, con una varianza de 1.02×10^{-4}, una desviación estándar de 0.0101 y un coeficiente de variación de 0.0629 (Tabla 14). Esto significa que durante el tiempo de la exploración, 16.04 % de las hembras maduras desovaron cada día o que cada hembra madura desovó, en promedio, cada 6.2 días. Mayores detalles referentes a la fracción de hembras maduras desovantes se da en Alarcón et al. (en prensa) y Alheit et al. (1984).

Producción diaria de huevos en el mar.

La computación iterativa de la producción diaria de huevos en el área investigada (P_0) y el coeficiente de mortalidad diaria de huevos (Z) fue desarrollado por medio de un programa de computadora desarrollada por U. Damm. La Z fue de 1.04. Esto implica una mortalidad de 65 % por día. La producción diaria de huevos en el area investigada fue de 6.4963×10^{13} huevos, con una varianza de 3.0496×10^{26}, una desviación estándar de 1.7463×10^{13} y un coeficiente de variación de 0.2688 (Tabla 14).

Estimado de biomasa desovante.

Los estimados de los cinco parámetros son listados en la Tabla 14. Usando la ecuación (15), la biomasa desovante fue estimada en la siguiente [illegible]

$$P \;\text{[illegible]}\; \frac{W}{\text{[illegible]}\,F\,\text{[illegible]}}$$

$$= \frac{(6.4963 \;\text{[illegible]})}{0.5643 : 0.1604 \;\; 15401}$$

$$= 1\,204{,}191 \text{ (toneladas métricas)}$$

La biomasa desovante de la subárea [illegible] norte y central de la anchoveta peruana en agosto-setiembre de 1981 fue de 1 204,191 toneladas métricas (Tabla 14). Asumiendo que todos los términos de covarianza en la ecuación (16) son cero, la varianza aproximada de B es 1.17×10^{11}. La desviación estándar y el coeficiente de variación son 341,485 toneladas y 0.2840 respectivamente (Tabla 14). Bajo la asunción que la varianza de B es simétrica, los límites de confianza aproximados a 95 % de B son ± 56.80 % de 1'204,191 toneladas métricas.

DISCUSION

Son evidentes las ventajas de la aplicación del "Método de Producción de Huevos" para estimar la biomasa desovante de peces pelágicos.

Una gran ventaja es el relativo bajo costo que requiere toda la aplicación del método por el tiempo relativamente corto de barco necesario para la toma de muestras.

Un factor muy importante es la posibilidad de conocer la precisión, siendo posible estimar el error independiente para cada uno de los 5 parámetros biológicos tratados, y la posibilidad de mejorar la precisión del estimado de la biomasa en forma efectiva, de acuerdo a los requerimientos y posibilidades económicas. Un aspecto importante es que se pueden calcular también los límites de confianza para el estimado de la biomasa. Los límites de confianza de 95 % de ± 57 % dan una precisión relativamente buena.

Otros métodos como el hidroacústico no rinden esta precisión. La dificultad más seria de los estimados de biomasa por el método hidroacústico en el sistema de afloramiento peruano es la co-ocurrencia de varias especies pelágicas en el mismo cardúmen, por lo que es bastante difícil discriminar por especies por el método hidroacústico si no se hace pesca de comprobación. Además la alta variación de la composición por especies de estos cardúmenes pelágicos requiere de una gran pesca de comprobación, la que a su vez incrementa los costos de barco considerablemente.

Otra de las grandes ventajas del "Método de Producción de Huevos" es que puede ser incorporada más de una especie en la investigación de la biomasa, por ejemplo anchoveta y sardina pueden hacerse juntamente sin aumentar más el tiempo de barco.

Una cuarta ventaja es que la investigación de la biomasa da la oportunidad de colectar además otros tipos de muestras biológicas sin mayor incremento de tiempo de barco, muestras como: fitoplacton, zooplancton, ictioplancton, contenido estomacal, otolitos etc., que permite estudios paralelos.

Una de las desventajas del "Método de Producción de Huevos" es que el procesamiento de las muestras en el laboratorio requiere de un número de horas/hombre de trabajo, relativamente alto lo que significa alrededor de 2 meses. La persona o personas que tienen que interpretar los cortes histológicos necesitan un entrenamiento especial.

El estimado final de biomasa de anchoveta para 1981, estuvo disponible después de 4 meses; sin embargo, esta fue la primera vez que este método fue aplicado en el Perú. En el futuro se espera que el tiempo entre el término del crucero de toma de muestras y el estimado final de la biomasa pueda ser reducido a 2 meses. Este es un período razonablemente breve que permite rápidas decisiones de manejo de las pesquerías.

De la Tabla 14 es evidente que los coeficientes de variación de los 4 parámetros para adultos son muy bajos y no necesitan ser mejorados. Una mayor intensidad de muestreo para adultos significaría pérdida de tiempo de barco y dinero. Sin embargo, la parte débil en el "Método de Producción de Huevos" parece ser el parámetro de producción diaria de huevos en el mar, (P_0). Este parámetro da la mayor contribución al coeficiente de variación del estimado de la biomasa. Lo que es causado por el tipo de distribución del desove de anchoveta (Santander **et al.** 1982). Mejoras futuras del estimado de error de los estimados de biomasa deben ser concentrados en este parámetro. Una posibilidad podría ser incrementar el número de muestras CalVET. Sin embargo, duplicar la precisión requiere cuatriplicar el número de muestras de huevos (Santander **et al.**, 1982). En 1981, 925 muestras CalVET se colectaron para las que se necesitaron 23 días de tiempo de barco. Si se incrementara el número de muestras CalVET deberá tomarse en cuenta el incremento en costos de tiempo de barco.

En el futuro sería ideal poder combinar el "Método de Producción de Huevos" para estimado de la biomasa desovante con los estimados hidroacústicos para obtener dos estimados independientes. Actualmente el "Método de Producción de Huevos" puede ser también aplicado a la sardina, **Sardinops sagax**. Alarcon **et al.** (1984) han obtenido por primera vez la clasificación y edad de los folículos post-ovulatorios de la sardina.

El más grande stock comercial en el mundo ahora está en el más bajo nivel registrado, de un décimo o menos que un décimo del tamaño del stock original de esta área. Según Tsukayama (1982) los puertos en las áreas norte y central del Perú desembarcaron un promedio de 8.1 millones de toneladas de anchoveta por año (rango de 6 - 11 millones de 1962 a 1971). En los 4 años más recientes (1978 - 81) con los datos disponibles los puertos en la misma área desembarcaron un promedio de 0.5 millones de toneladas (rango de 0.2 a 1.0). Considerando el estimado de la biomasa obtenida en setiembre de 1981 la captura de 0.5 millones de toneladas resulta ser una de las más grandes proporciones del stock desovante que se han capturado. Según Tsukayama (1982) en 1981 no se ha observado reclutamiento en esta área por lo que el stock desovante es también el stock total. El tamaño grande de algunas hembras indica que el stock remanente puede ser también viejo y en consecuencia entrar en un período de alta mortalidad natural como es común para clupeidos de más edad.

Los desembarques de 900,000 toneladas de anchoveta hasta setiembre de 1982 sin evidencia de reclutamiento (Tsukayama, comunicación personal) podrían significar una seria depauperización del stock. Esto es reminiscente de la situación de la sardina de California; una población de 4 millones de toneladas reducida a menos de 10,000 toneladas en 1965, sin que se haya percibido recuperación hasta 1981. Una pesquería adicional en el agotado stock de anchoveta de las áreas norte y central del Perú probablemente causaría mayor dilación en la recuperación de un stock del que se capturaba varios millones de toneladas por año en este habitat.

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ANEXO I

DESCRIPCION DEL DESARROLLO EMBRIONARIO DE ANCHOVETA EN ESTADIOS

Estadío I	En este estadío están incluidos los huevos de anchoveta recientemente desovados, en los que no se ha iniciado la división celular. Hay una acumulación conspicua de citoplasma en el polo animal que forma una capa, el BLASTODISCO.
Estadío II	Es el período de desarrollo de la capa blastodérmica y la iniciación de la división celular, en 2, 4, 8 células, hasta la agregación de células que toman apariencia de mórula. Se considera este estadío hasta que se produce la segmentación de la cavidad (i.e. Gastrulación) la que es difícilmente observable en huevos preservados por ser una estructura interna.
Estadío III	Este estadío comprende el período de desarrollo, desde la primera aparición de la segmentación de la cavidad hasta el establecimiento definitivo de la cubierta embrionaria. El blastodermo comienza encerrando el vitelo por EPIBOLIA. Al final de este estadío, el blastodermo se extiende hacia abajo, cerca de 1/3 de la longitud del vitelo.
Estadío IV	Este estadío es más fácilmente identificado por la extensión de la cubierta del vitelo por el blastodermo. Se inicia cuando la cubierta blastodérmica está cerca de 1/3 del vitelo y finaliza cuando la cubierta blastodérmica está cerca de 2/3 del vitelo. Ya se puede notar la zona de desarrollo del embrión, pero no hay rasgos distintivos semejantes como los ojos, que están aún en desarrollo.
Estadío V	Este estadío comienza cuando el blastodermo ha cubierto aproximadamente 2/3 del vitelo y finaliza con el cierre del BLASTOPORO. El desarrollo de los ojos puede ser visto en la cabeza al final de este estadío, y los MIOMEROS están comenzando a formarse a lo largo del cuerpo del embrión.
Estadío VI	Comienza con el movimiento del cierre del blastoporo y termina en el momento que la porción de la cola del embrión empieza a separarse del vitelo. Estadíos posteriores, de VII a XI, están separados principalmente por el grado de desarrollo de la cola libre, que ofrece una mejor señal para la separación de los estadíos.
Estadío VII	Este estadío se inicia cuando la cola principia a separarse de la masa vitelina; e incluye el crecimiento inicial de la cola hasta que la porción libre es de alrededor de 1/2 de la longitud de la cabeza del embrión. La porción libre de la cola permanece en el mismo plano que el cuerpo.
Estadío VIII	Al principio de este estadío, la cola en desarrollo comienza a doblarse hacia afuera del eje del cuerpo y concluye con una tendencia hacia 180^{o} con esta porción posterior creciendo hacia la cabeza. Al final de este estadío, la porción libre de la cola es cerca de 1/5 de la longitud del saco vitelino.
Estadío IX	La torsión de la cola, algo arbitraria, comienza cuando la separación de la cola es igual a la longitud de la cabeza y de 1/4 a 1/2 del vitelo. La torsión se produce fuera del plano del embrión.
Estadío X	La cola se aproxima a la cabeza por encima del tronco. Al comienzo, es de 2 veces la longitud de la cabeza y la longitud de la cola libre es igual a 1/2 del vitelo.

Estadío XI La longitud de la cola libre es mayor que 3/4 la longitud del vitelo. Se asume que la longitud de la cabeza es aproximadamente igual a 1/4 de la longitud del vitelo.

ANEXO II

Hay varias alternativas para ajustar curvas no lineales. Los métodos dependen de la asunción de los datos básicos y de la calidad de las proyecciones e interpolaciones. Después de considerar la magnitud del problema del trabajo especializado sobre una curva apropiada, los autores decidieron usar un programa simple escrito por U. Damm, comparando los resultados con los resultados publicados de otras aproximaciones y ádaptándolos para su uso en este trabajo. Se decidió publicar el programa con este manuscrito con la esperanza que el proceso iterativo de ajuste de la curva no lineal será especificado más completamente en relación a la sensibilidad de cambios en varianza a través del período de la curva y de las distorciones en la ponderación de observaciones por transformación a logaritmos y aplicando una regresión lineal. Una característica de este conjunto de datos es que los huevos son depositados en parches intensos y son rápidamente dispersos fuera de los centros. Puesto que el principal objetivo de este trabajo es encontrar el intercepto de una curva de mortalidad exponencial, hemos preferido usar los datos originales más que arriesgar una subestimación usando una regresión logarítmica lineal.

El programa está trazado para ser introducido en una microcomputadora Tandy TRS-80 Modelo III con 16 K de memoria y de lenguaje BASIC. El programa original escrito por Damm usó solamente precisión aritmética. Este programa ha sido convertido a precisión doble (17 dígitos significativos) porque 7 dígitos significativos pueden no ser suficientes para exponenciación y potenciación de los valores de las muestras y errores derivados.

Las dimensiones del programa, el número de pares de observaciones en la línea 200 y la sección de entrada es desde la instrucción 210 a la 240. En la línea 250 la relación entre el intervalo escogido y la unidad de la salida es seleccionada. Por ejemplo, el muestreo cada 8 horas con una tasa expresada en número por día requerirá la respuesta 0.33333. Si el resultado fuera en decrecimiento en unidades por hora y el intervalo de muestreo fuera 8 horas, la respuesta al intervalo relativo de unidad de tiempo sería 8.

Los valores iniciales se han establecido para dar una pendiente de prueba "Z" en la instrucción 270 e instrucciones 280-290. El procedimiento iterativo se inicia en la línea 300, haciendo un cambio fraccional en"Z" y comparando la diferencia, siguiendo la llamada a la subrutina, de desviación que se inicia en la línea 500.

En la línea 335 el cambio de valores es comparado y si éste es menor que una parte en 100,000, los parámetros finales son seleccionados. Si la diferencia es mayor que 100,000, la iteración es ejecutada nuevamente. Siguiendo la aceptación eventual de un cambio insignificativo, los cálculos del error final son determinados en las instrucciones 370 a 490 e impresos en las instrucciones 492 para el valor y error del intercepto, y 494 para el valor y error de la pendiente exponencial

El programa ha sido comparado favorablemente con procedimientos más complicados usando la misma clase de datos. Estos programas toman pocos minutos para ser ejecutados.

Tabla 1a. "Tabla de Decisión" para determinar a bordo cuántos peces deben ser colectados de cada captura. Dependiendo del número de hembras entre los primeros 10 ejemplares, 10 ó 20 ejemplares deben ser sexados. Todos los peces de los frascos adicionales no son sexados a bordo. Cada recipiente contiene 5 ejemplares.

No. DE HEMBRAS ENCONTRADO	DECISION DESPUES DE SEXAR 10 EJEMPLARES	DECISION DESPUES DE SEXAR 20 JEMPLARES
1	Sexar 10 ejemplares más	20 recipientes adicionales son necesarios
2	,,	20 ,,
3	,,	20 ,,
4	,,	20 ,,
5	,,	20 ,,
6	,,	20 ,,
7	,,	20 ,,
8	8 recipientes adicionales son necesarios	18 ,,
9	6 ,,	14 ,,
10	5 ,,	11 ,,
11		9 ,,
12		7 ,,
13		6 ,,
14		5 ,,

Tabla 1b. Número total de recipientes necesarios y número total de ejemplares a preservar, de acuerdo al número de hembras encontradas entre los primeros 10 ó 20 ejemplares sexados.

	No. DE HEMBRAS ENCONTRADOS	No. TOTAL DE RECIPIENTES	No. TOTAL DE EJEMPLARES PRESERVADOS
Después de sexar 10 ejemplares	8	8 + 2	50
	9	6 + 2	40
	10	5 + 2	35
	1 – 7	20 + 4	120
	8	18 + 4	110
	9	14 + 4	90
Después de sexar 20 ejemplares	10	11 + 4	75
	11	9 + 4	65
	12	7 + 4	55
	13	6 + 4	50
	⩾ 14	5 + 4	45

Tabla 2. Peso total y peso sin gonada de 238 hembras. Esta serie de datos fue usada para establecer la regresión lineal entre peso total y peso de hembra sin gonada.

PESO TOTAL	PESO SIN GONADA	PESO TOTAL	PESO SIN GONADA	PESO TOTAL	PESO SIN GONADA
16.06	15.51	23.11	21.97	32.07	30.72
12.90	12.27	29.33	26.99	24.33	23.31
19.79	19.10	25.37	23.07	20.71	19.66
25.24	24.50	40.37	37.98	34.22	31.68
30.40	28.45	23.69	22.41	21.94	21.06
44.48	40.47	40.94	37.70	21.81	20.96
30.77	29.02	28.96	26.99	32.83	31.02
31.13	28.99	27.79	25.90	42.57	39.80
34.79	33.03	26.99	25.73	31.89	30.79
28.91	26.49	21.71	20.60	20.57	19.49
37.97	35.81	28.50	26.32	31.89	30.28
38.62	36.38	42.49	38.49	19.39	18.79
26.58	25.56	25.40	24.12	21.47	20.30
43.13	40.01	35.89	34.61	30.29	28.78
35.86	34.17	30.33	28.09	29.55	27.69
25.87	24.19	31.16	29.78	34.71	33.07
22.01	21.07	35.65	34.23	37.55	35.61
23.14	22.03	30.74	28.56	33.63	31.62
18.22	16.89	31.24	29.34	43.80	41.42
21.78	20.71	25.50	24.44	37.39	35.20
23.76	22.36	25.61	24.16	32.92	31.21
25.12	23.59	23.52	23.28	36.14	33.91
19.77	19.41	27.57	24.99	41.73	39.10
19.07	17.57	17.22	15.95	27.70	26.39
17.65	16.88	27.61	26.40	20.64	18.95
23.30	22.16	28.65	27.11	22.45	21.11
21.47	19.98	30.86	28.81	25.63	24.53
32.10	30.46	44.56	41.11	21.33	20.32
35.45	33.99	24.17	22.75	35.00	33.45
32.25	30.55	31.79	29.95	44.35	41.97
32.48	30.98	23.70	22.79	21.73	20.19
35.26	33.64	26.16	24.55	32.[illegible]	31.[illegible]
32.05	30.96	26.10	24.91	16.2[illegible]	15.4[illegible]
45.39	42.61	43.84	41.75	16.6[illegible]	16.[illegible]
27.96	26.53	40.80	38.47	16.89	16.2[illegible]
33.87	32.45	41.30	39.20	19.88	19.34
22.31	21.36	25.86	24.35	17.04	16.43
22.73	21.52	27.49	26.24	18.79	18.22
26.75	25.69	35.77	34.30	19.65	19.24
24.01	22.77	32.94	31.20	18.65	18.05
40.16	38.23	32.26	30.24	17.20	16.95
30.08	28.04	30.03	28.34	19.82	19.46
25.87	24.85	31.88	30.35	19.94	19.25
47.88	45.83	28.95	27.73	27.02	25.34
28.76	27.24	23.53	22.67	34.01	32.84
32.44	30.28	22.39	21.35	38.21	36.38
34.83	32.82	36.55	33.89	35.62	33.59
34.61	32.36	34.71	32.86	29.40	27.94

Tabla 2. (Continuación)

29.42	27.47	27.86	26.13	17.64	16.84
34.32	32.68	20.26	19.50	20.45	19.73
20.57	19.79	23.77	22.95	19.45	18.58
17.46	17.15	22.20	21.16	17.59	16.63
18.50	17.78	20.29	18.89	17.30	16.89
36.38	34.30	20.30	19.53	15.00	14.53
26.32	25.32	18.66	18.01	20.80	20.08
23.27	22.05	20.76	20.28	23.34	22.04
31.28	29.81	27.66	26.76	32.35	31.20
31.67	30.54	15.53	14.74	21.90	20.97
24.37	23.03	11.39	10.96	24.26	23.17
36.05	34.18	8.46	8.01	17.17	16.33
32.65	30.78	9.57	9.34	36.50	34.81
28.05	27.08	10.95	10.71	38.66	35.24
29.12	27.47	17.49	16.92	33.97	31.38
37.21	35.87	20.25	19.38	18.65	17.93
40.88	38.47	20.17	19.05	30.11	28.83
27.59	36.38	32.01	30.33	21.21	20.11
21.60	21.04	15.71	15.02	19.97	18.77
26.55	25.18	20.69	20.20	25.41	24.32
32.59	31.31	35.45	33.51	24.81	23.85
21.32	20.14	31.08	30.14	19.57	18.77
16.80	16.21	20.00	19.09	32.37	30.62
29.76	28.58	20.86	19.76	38.28	36.52
31.53	29.82	21.33	20.61	35.67	34.07
44.80	41.72	24.13	23.40	19.47	18.36
32.07	31.27	21.89	21.11	20.72	19.81
18.66	18.13	20.73	19.79	21.43	20.20
16.00	14.61	20.25	19.43	21.10	20.03
19.51	18.83	24.35	22.60	28.75	27.03
30.40	28.99	32.06	30.64		
21.04	20.57	35.97	34.36		

Tabla 3. Fecundidad parcial y peso sin gonada de ~~105~~ ejemplares hembras. Esta serie de datos fue usada para establecer la regresión logarítmica doble entre fecundidad parcial y peso de hembras sin gonada.

FECUNDIDAD PARCIAL	PESO DE HEMBRAS	FECUNDIDAD PARCIAL	PESO DE HEMBRAS	FENCUNDIDAD PARCIAL	PESO DE HEMBRAS
14372	26.62	7524	18.59	7257	15.57
13483	22.24	12488	24.49	5977	16.84
20479	29.33	19884	34.48	10161	25.56
19055	29.79	9003	21.35	9921	21.13
15718	27.82	10379	23.83	14209	26.72
18077	24.24	6272	17.73	11937	32.28
25122	30.52	9410	21.23	10808	26.82
17863	24.93	7838	20.35	18090	34.02
17110	25.82	11336	25.82	9330	23.18
15460	22.38	11379	21.94	21954	29.56
10963	26.68	19567	28.99	16357	21.66
29621	35.04	8601	20.50	22138	26.33
17937	27.92	11528	29.59	20434	30.16
18707	24.97	17324	25.71	13797	24.44
14142	24.97	6651	18.32	12748	20.78
19191	25.02	12956	21.44	10415	24.16
15106	30.20	15812	30.09	13032	26.06
14893	22.49	20550	30.80	18077	25.58
12297	21.94	17720	28.31	13836	26.78
10600	19.54	20962	34.09	23268	34.15
16232	28.51	17959	27.21	9034	20.02
10926	23.04	17710	27.07	14243	24.36
22235	28.52	15272	28.73	24479	31.14
25814	33.23	22469	40.26	9130	22.71
16650	26.59	17620	29.44	5613	17.39
16771	27.09	20934	27.55	8811	18.27
10025	24.20	13120	34.27	14089	24.70
17973	24.77	16071	28.10	3847	12.69
12538	27.27	19789	35.66	7936	17.87
18179	26.10	15340	28.08	6147	13.88
21390	30.59	20267	34.93	22386	36.39
29013	37.38	21738	33.15	7251	16.45
17122	21.73	22288	31.90	6518	15.77
17421	21.96	19941	35.46		
16883	24.30	15816	33.75		
20834	25.81	26251	28.50		
20721	29.96	6380	14.88		

Tabla 4. Resumen de 1) Número 2) Fecha 3) Hora 4) Posición de colección 5) Peso promedio de hembras maduras en gramos 6) Fecundidad parcial en huevos por hembra y 7) Proporción de hembras en la población basado en el peso (Proporción sexual).

NUMERO DE COLECCION	FECHA	HORA	POSICION		PESO PROMEDIO DE HEMBRAS	PROMEDIO DE FECUNDIDAD PARCIAL	PROPORCION SEXUAL
			LATITUD S	LONGITUD W			
1	25.8	03.15	13°03’	76°35’	19.75	9 511	.5142
2	25.8	12.00	13°38’	76°38’	30.29	19 347	.6895
3	25.8	16.30	13°28’	76°39’	31.05	20 763	.7442
4	25.8	19.30	13°26’	76°19’	25.59	14 625	.5533
5	26.8	09.00	13°10’	76°29’	23.63	12 752	.4496
6	26.8	15.30	12°44’	77°04’	26.16	15 054	.8127
7	26.8	19.30	12°20’	76°56’	30.94	20 426	.5828
8	27.8	18.00	12°01’	77°21’	25.33	14 314	.4521
10	28.8	09.00	12°55’	77°52’	30.10	20 340	.3151
11	28.8	14.15	12°38’	76°50’	29.13	18 289	.4743
12	28.8	19.30	12°50’	76°42’	25.98	14 866	.1262
15	29.8	16.00	12°32’	76°54’	30.12	19 424	.3257
16	29.8	19.30	12°38’	76°51’	26.58	15 496	.4393
17	30.8	09.30	12°18’	77°14’	32.43	22 101	.5444
18	30.8	13.00	12°14’	77°07’	27.31	16 531	.5532
19	30.8	19.15	12°08’	77°13’	27.76	17 273	.4613
20	31.8	16.15	12°06’	77°22’	26.52	15 597	.2636
21	31.8	22.45	11°50’	77°18’	30.14	20 447	.7968
22	1.9	10.00	11°34’	77°28’	30.68	20 152	.6733
23	1.9	16.45	11°34’	77°37’	26.99	16 199	.7873
24	1.9	19.00	11°27’	77°38’	24.33	13 624	.6038
25	1.9	21.00	11°32’	77°22’	25.18	14 726	.7868
26	2.9	08.30	11°39’	77°18’	24.41	14 105	.6874
27	2.9	12.30	11°45’	77°17’	30.83	20 277	.4989
28	5.9	07.15	11°14’	77°48’	36.78	27 408	.5276
29	5.9	09.15	11°15’	77°54’	25.65	14 891	.9050
31	5.9	18.15	10°56’	78°00’	25.83	15 558	.6715
32	5.9	21.15	10°43’	77°54’	18.29	8 180	.6418
33	6.9	08.00	10°56’	77°46’	18.68	8 822	.8301
34	7.9	12.10	10°35’	78°07’	32.14	21 714	.7096
35	7.9	14.45	10°26’	78°01’	18.59	8 435	.7051
36	7.9	18.00	10°27’	78°12’	25.83	15 044	.3611
37	7.9	22.55	10°11’	78°10’	26.07	15 294	.6436
38	8.9	07.25	10°06’	78°12’	26.90	16 387	.5530
40	8.9	16.10	09°52’	78°16’	26.39	16 180	.6038
41	8.9	20.15	09°42’	78°22’	32.38	22 124	.1586
42	9.9	09.00	09°37’	78°28’	23.69	13 317	.3338
44	9.9	17.10	09°22’	78°29’	18.75	8 711	.6212
45	9.9	20.10	09°06’	78°43’	25.35	14 848	.7393
46	11.9	18.00	08°34’	78°59’	22.05	11 947	.2990
47	11.9	21.00	08°27’	79°02’	22.46	11 908	.7920
48	12.9	08.45	07°37’	79°37’	21.18	10 461	.4532
49	12.9	13.15	07°25’	79°43’	19.80	9 515	.5929
52	16.9	10.10	08°07’	79°12’	12.29	4 154	.4580
53	16.9	13.10	07°55’	79°26’	23.42	12 955	.6204
54	16.9	17.35	07°48’	79°35’	25.83	15 441	.7194
55	16.9	19.40	07°43’	79°39’	23.24	12 605	.6552
57	17.9	12.00	08°11’	79°30’	32.50	22 451	.6362
58	17.9	14.15	08°19’	79°19’	20.65	10 060	.2818

Tabla 5. Valores de t_i y t_i' $\left(= t_i - \dfrac{t_1 + t_o}{2}\right)$

(a) HORA	t_i EN HORAS			(b) t_i' EN HORAS		EN FRACCION DE DIA
18.00	t_o	=	0			
02.00	t_1	=	8	t_1'	4	0.1667
14.00	t_2	=	20	t_2'	16	0.6667
02.00	t_3	=	32	t_3'	28	1.1667
14.00	t_4	=	44	t_4'	40	1.6667

Tabla 6. Ejemplo de uso de datos para determinación de edad en huevos.

ESTADIO	NUMERO DE HUEVOS	CATEGORIA DE EDAD ASIGNADA	No. TOTAL EN CATEGORIA DE EDAD	
I	0			
II	14	A	A	45
III	31	A		
IV	0			
V	6	B		
VI	22	B	B	36
VII	8	B		
VIII	0			
IX	1	C		
X	3	C	C	5
XI	1	C		
Dis	11		Dis	11
TOTAL				97

Tabla 7. Dimensiones de regiones exploradas y número de unidades de muestreo (0.05 m^2) en cada región.

REGION	DIMENSIONES (mn) A LO LARGO DE LA COSTA	DISTANTE DE LA COSTA	AREA MILLAS CUADRADAS	UNIDADES DE MUESTREO
11	170	33	5610	3.8484×10^{11}
11 (costera)	170	5	850	5.8308×10^{10}
21	180	33	5940	4.0747×10^{11}
21 (Costera)	180	5	900	6.1738×10^{10}
31	180	33	5940	4.0747×10^{11}
31 (Costera)	180	5	900	6.1738×10^{10}
12	170	30	5100	3.4985×10^{11}
22	180	30	5400	3.7043×10^{11}
32	180	30	5400	3.7043×10^{11}
13	170	30	5100	3.4985×10^{11}
23	180	30	5400	3.7043×10^{11}
33	180	30	5400	3.7043×10^{11}
TOTAL			52240	

Tabla 8. Resumen de datos de huevos

1 CATEGORIAS DE EDAD	2 REGION	3 No. DE ESTACIONES	4 No. TOTAL DE HUEVOS COLECTADOS POR REGION	5 No. PROMEDIO DE HUEVOS POR ESTACION	6 No. DE UNIDADES DE MUESTREO ($\times 10^{11}$)	7 No.TOTAL DE HUEVOS POR REGION ($\times 10^{12}$)	8 No. TOTAL DE HUEVOS POR CATEGORIA DE EDAD
S	11	83	20	0.24	3.8484	0.0924	12.5365×10^{12}
	21	89	1114	12.52	4.0747	5.1015	
	22	23	5	0.22	3.7043	0.0815	
	31	105	1871	17.82	4.0747	7.2611	
A_1	11	104	2625	25.24	3.8484	9.7134	38.9720×10^{12}
	21	108	4432	41.04	4.0747	16.7226	
	22	37	6	0.16	3.7043	0.0593	
	31	86	2633	30.62	4.0747	12.4767	
A_2	11	83	406	4.89	3.8484	1.8819	15.3988×10^{12}
	21	89.	1744	19.60	4.0747	7.9864	
	22	23	17	0.74	3.7043	0.2741	
	31	105	1354	12.90	4.0747	5.2564	
B_1	11	104	779	7.49	3.8484	2.8825	19.4554×10^{12}
	21	108	2555	23.66	4.0747	2.6407	
	22	37	7	0.19	3.7043	0.0704	
	31	86	1448	16.84	4.0747	6.8618	
B_2	11	83	177	2.13	3.8484	0.8197	6.0638×10^{12}
	21	89	535	6.01	4.0747	2.4489	
	22	23	0	0.00	3.7043	0.0000	
	31	105	720	6.86	4.0747	2.7952	
C_1	11	104	35	0.34	3.8484	0.1308	3.2979×10^{12}
	21	108	342	3.17	4.0747	1.2917	
	22	37	3	0.08	3.7043	0.0296	
	31	86	390	4.53	4.0747	1.8458	
C_2	11	83	2	0.02	3.8484	0.0077	0.0811×10^{12}
	21	89	8	0.09	4.0747	0.0367	
	22	23	0	0.00	3.7043	0.0000	
	31	105	9	0.09	4.0747	0.0367	
Dis_1	11	104	155	1.49	3.8484	0.5734	2.3825×10^{12}
	21	108	131	1.21	4.0747	0.4930	
	22	37	0	0.00	3.7043	0.0000	
	31	86	278	3.23	4.0747	1.3161	
Dis_2	11	83	41	0.49	3.8484	0.1886	3.2228×10^{12}
	21	89	176	1.98	4.0747	0.8068	
	22	23	1	0.04	3.7043	0.0148	
	31	105	570	5.43	4.0747	2.2126	

Tabla 9. Distribución de huevos "Dis" en categorías de edad. Número total de huevos "Dis 1": 2.3825 x 10^{12} (Tabla 8). Número total de huevos "Dis 2": 3.2228 x 10^{12}

1 CATEGORIA DE EDAD	2 No. DE HUEVOS (x 10^{12})	3 PROPORCION (%)	4 No. DE HUEVOS "Dis" (x 10^{12})	5 No. TOTAL DE HUEVOS (x 10^{12})
A_1	38.9720	63.14	1.5043	40.4763
B_1	19.4554	31.52	0.7510	20.2064
C_1	3.2979	5.34	0.1272	3.4251
S	12.5365	36.79	1.1857	13.7222
A_2	15.3988	45.18	1.4561	16.8549
B_2	6.0638	17.79	0.5733	6.6371
C_2	0.0811	0.24	0.0077	0.0888

Tabla 10. Distribución de huevos "cercanos a la costa" y número total de huevos por categorías de edad.

1 CATEGORIA DE EDAD	2 No. DE HUEVOS* (x 10^{12})	3 PROPORCION (%)	4 No. DE HUEVOS CERCANOS A LA COSTA (x 10^{12})	5 No. TOTAL DE HUEVOS (x 10^{12})	P_i
S	13.7222	13.53	1.3524	15.0746	
A_1	40.4763	39.91	3.9892	44.4655	
A_2	16.8549	16.62	1.6613	18.5162	
B_1	20.2064	19.93	1.9921	22.1985	
B_2	6.6371	6.54	0.6537	7.2908	
C_1	3.4251	3.38	0.3379	3.7630	
C_2	0.0888	0.09	0.0090	0.0978	
TOTAL	101.4108	100.00	9.9956	111.4064	

* De la Tabla 9.

Tabla 11. Valores de t_i' y P_i

t_i'	CATEGORIA DE EDAD	P_i*
0.1667	A_1	44.4655 x 10^{12}
0.6667	A_2	18.5162 x 10^{12}
1.1667	B_1	22.1985 x 10^{12}
1.6667	B_2	7.2908 x 10^{12}

* De la Tabla 10.

Tabla 12. Edad de folículos post-ovulatorios.

	HORA	EDAD DE FOLICULOS POST-OVULATORIOS (Horas después de desove)	
		HEMBRAS Día-1	HEMBRAS Día-2
NOCHE DE DESOVE	22.00 PICO DE DESOVE	0	0
Día siguiente al de desove	07.00 - 07.59	9	33
	08.00 - 08.59	10	34
	09.00 - 09.59	11	35
	10.00 - 10.59	12	36
	11.00 - 11.59	13	37
	12.00 - 12.59	14	38
	13.00 - 13.59	15	39
	14.00 - 14.59	16	40
	15.00 - 15.59	17	41
	16.00 - 16.59	18	42
	17.00 - 17.59	19	43
	18.00 - 18.59	20	44
	19.00 - 19.59	21	45
	20.00 - 20.59	22	46
	21.00 - 21.59	23	47
	22.00 - 22.59	24	48
	23.00 - 23.59	25	49
2do. día siguiente al de desove	00.00 - 00.59	26	50
	01.00 - 01.59	27	51
	02.00 - 02.59	28	52
	03.00 - 03.59	29	53
	04.00 - 04.59	30	54
	05.00 - 05.59	31	55
	06.00 - 06.59	32	56

[illegible] fracción de hembras desovantes por día.

No. De COLECCION	HORA	HEMBRAS HIDRATADAS		HEMBRAS DIA-1		HEMBRAS DIA-2		$\frac{m_{1i} + m_{2i}}{2}$	m_{ai}	m_{yi}	$\hat{F}$	$\hat{F}$	$\left(\frac{m_{yi}}{m}\right)^2 \times (\hat{F} - \bar{F})^2$	
		No. (m_{hi})	%	Horas después del desove	No. (m_{1i})	Horas después del desove	No. (m_{2i})				Dia-1 (m_{1i}/m_{yi})	Dia-2 (m_{2i} m_{yi})	Día-1	Día-2
28	07.15	11	55	9	0	33	0	0	9	9.0	0	0	.0062	.0062
38	07.25	3	15	9	3	33	3	3.0	11	20.0	.1500	.1500	.0001	.0001
33	08.00	0	0	10	2	34	1	1.5	17	21.5	0930	.0465	.0062	.0178
26	08.30	0	0	10	2	34	4	3.0	14	23.0	0870	.1739	.0085	.0003
48	08.45	5	25	10	6	34	3	4.5	6	19.5	.3077	.1538	.0246	0
5	09.00	11	55	11	2	35	1	1.5	6	10.5	1905	.0952	.0003	.0014
10	09.00	7	35	11	6	35	1	3.5	6	16.5	.3636	.0606	.0335	.0081
42	09.00	2	10	11	0	35	0	0	18	18.0	0	0	.0248	.0248
29	09.15	2	10	11	2	35	3	2.5	13	20.5	.0976	.1463	.0049	.0002
17	09.30	10	50	11	2	35	0	1.0	8	11.0	.1818	0	.0002	.0093
22	10.00	0	0	12	2	36	1	1.5	17	21.5	.0930	.0465	.0062	.0178
52	10.10	3	15	12	6	36	3	4.5	8	21.5	.2791	.1395	.0194	.0006
2	12.00	2	10	14	5	38	3	4.0	10	22.0	.2273	.1364	.0064	.0008
57	12.00	2	10	14	6	38	5	5.5	7	23.5	.2553	.2128	.0148	.0045
34	12.10	10	50	14	3	38	0	1.5	7	11.5	.2609	0	.0040	.0101
27	12.30	6	30	14	1	38	2	1.5	11	15.5	.0645	.1290	.0066	.0007
18	13.00	3	15	15	2	39	2	2.0	13	19.0	.1053	.1053	.0033	.0033
53	13.10	4	20	15	6	39	3	4.5	7	20.5	.2927	.1463	.0219	.0002
49	13.15	2	10	15	4	39	2	3.0	12	21.0	.1905	.0952	.0012	.0056
11	14.15	3	15	16	4	40	4	4.0	9	21.0	.1905	.1905	.0012	.0012
58	14.15	11	55	16	1	40	1	1.0	7	10.0	.1000	.1000	.0011	.0011
35	14.45	3	15	16	0	40	6	3.0	11	20.0	0	.3000	.0306	.0232
6	15.30	2	10	17	9	41	1	5.0	8	23.0	.3913	.0435	.0839	.0215
15	16.00	5	25	18	1	42	3	2.0	11	17.0	.0588	.1765	.0089	.0002
40	16.10	1	5	18	3	42	5	4.0	11	23.0	.1304	.2174	.0014	.0051
20	16.15	3	15	18	4	42	6	5.0	7	22.0	.1818	.2727	.0007	.0182
3	16.30	0	0	18	4	42	7	5.5	9	25 5	.1569	.2745	0	.0252
23	16.45	0	0	18	6	42	4	5.0	10	25.0	.2400	.1600	.0118	0
44	17.10	2	10	19	1	43	3	2.0	14	20.0	.0500	.1500	.0145	.0001
54	17.35	6	30	19	7	43	4	5.5	3	19.5	.3590	.2051	.0446	.0023
8	18.00	1	5	20	1	44	1	1.0	17	20.0	.0500	.0500	.0145	.0145
36	18.00	13	65	20	2	44	4	3.0	1	10.0	.2000	.4000	.0005	.0171
46	18.00	16	80	20	1	44	0	0.5	3	4.5	2222	0	.0002	.0016

31	18.15	2	10	20	5	44	1	3.0	12	21.0	.2381	.0476	.0079	.0167
24	19.00	3	15	21	1	45	2	1.5	14	18.5	.0541	.1081	.0115	.0028
19	19.15	4	20	21	4	45	7	5.5	5	21.5	.1860	.3256	.0009	.0375
4	19.30	13	65	21	3	45	0	1.5	4	8.5	.3529	0	.0080	.0055
7	19.30	2	10	21	2	45	4	3.0	12	21.0	.0952	.1905	.0056	.0012
12	19.30	17	85	21	0	45	0	0	3	3.0	0	0	.0007	.0007
16	19.30	8	40	21	3	45	3	3.0	6	15.0	.2000	.2000	.0011	.0011
55	19.40	2	10	21	1	45	5	3.0	12	21.0	.0476	.2381	.0167	.0079
45	20.10	1	5	22	5	46	6	5.5	8	24.5	.2041	.2449	.0034	.0128
41	20.15	19	95	22	0	46	0	0	1	1.0	0	0	.0001	.0001
25	21.00	2	10	23	4	47	7	5.5	7	23.5	.1702	.2979	.0002	.0311
47	21.00	0	0	23	4	47	4	4.0	12	24.0	.1667	.1667	.0001	.0001
32	21.15	0	0	23	2	47	2	2.0	16	22.0	.0909	.0909	.0070	.0070
21	22.30	1	5	24	3	48	4	3.5	12	22.5	.1333	.1778	.0011	.0005
37	22.55	1	5	24	9	48	1	5.0	9	24.0	.3750	.0417	.0790	.0242
1	03.15	2	10	29	5	53	1	3.0	12	21.0	.2381	.0476	.0079	.0167

Tabla 14. Parámetros estimados y estimado de la biomasa desovante con varianzas asociadas ($V_{\hat{x}}$), desviaciones estándar ($SD_{\hat{x}}$), coeficiente de variación ($CV_{\hat{x}}$).

SIMBOLO	PARAMETRO	$\hat{x}$	$V_{\hat{x}}$	$SD_{\hat{x}}$	$CV_{\hat{x}}$
P_o	Producción diaria de huevos en área investigada	6.4963×10^{13}	3.0496×10^{26}	1.7463×10^{13}	0.2688
W	Peso promedio de hembras	25.84 g	0.4494	0.6704	0.0259
R	Fracción de hembras	0.5643	0.0007	0.0259	0.0459
E	Fecundidad parcial (huevos/hembra)	15 401	4.32×10^{5}	657.3	0.0427
F	Fracción de hembras que desova por día	0.1604	1.02×10^{-4}	0.0101	0.0629
B	Biomasa desovante (ton. métricas)	1 204 191	1.17×10^{11}	3.42×10^{5}	0.2840

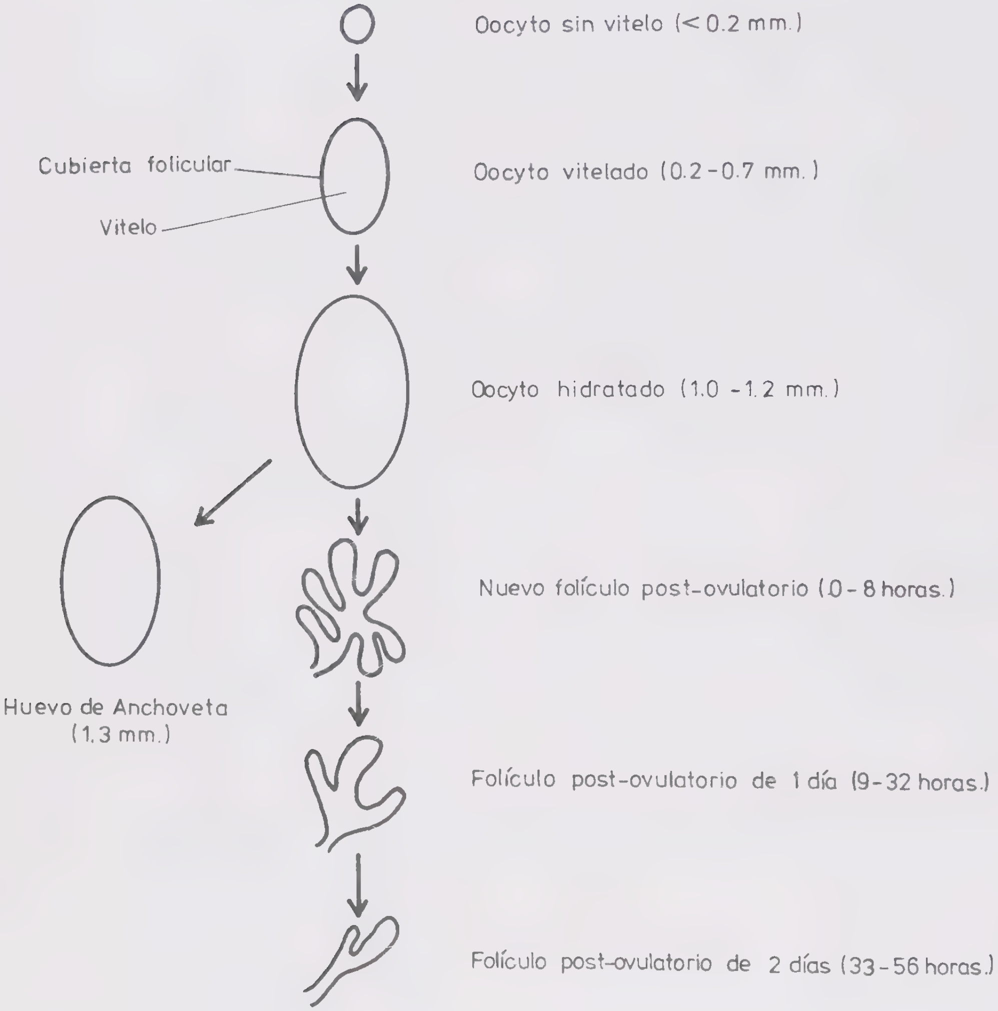
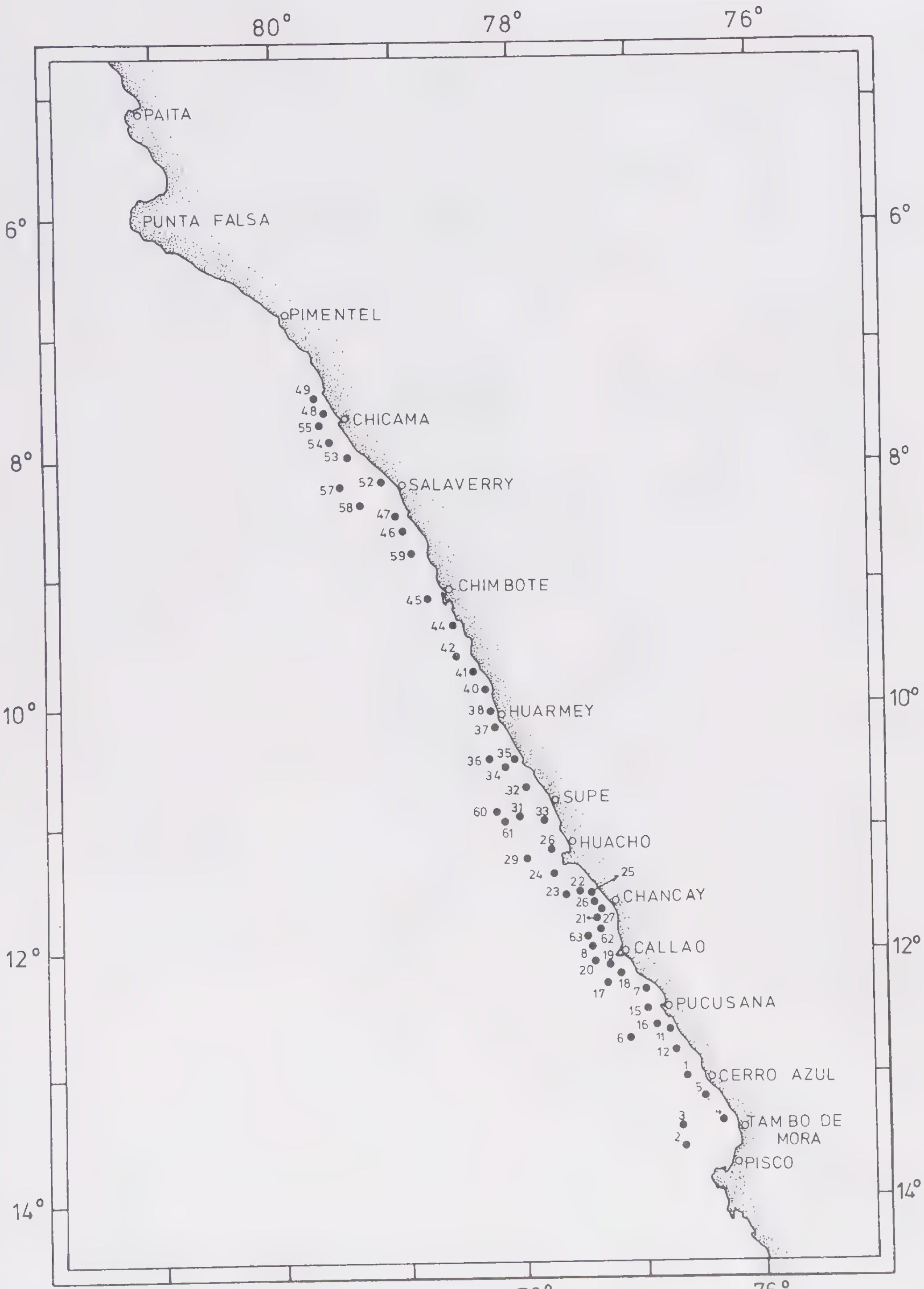

Oocyto sin vitelo (< 0.2 mm.)
Cubierta folicular
Vitelo
Oocyto vitelado (0.2 - 0.7 mm.)
Oocyto hidratado (1.0 - 1.2 mm.)
Huevo de Anchoveta (1.3 mm.)
Nuevo folículo post-ovulatorio (0 - 8 horas.)
Folículo post-ovulatorio de 1 día (9 - 32 horas.)
Folículo post-ovulatorio de 2 días (33 - 56 horas.)

Fig. 1 Representación esquemática del desarrollo de oocitos y de folículos post-ovulatorios.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PUNTA FALSA
PIMENTEL
CHICAMA
SALAVERRY
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HUARMEY
SUPE
HUACHO
CHANCAY
CALLAO
PUCUSANA
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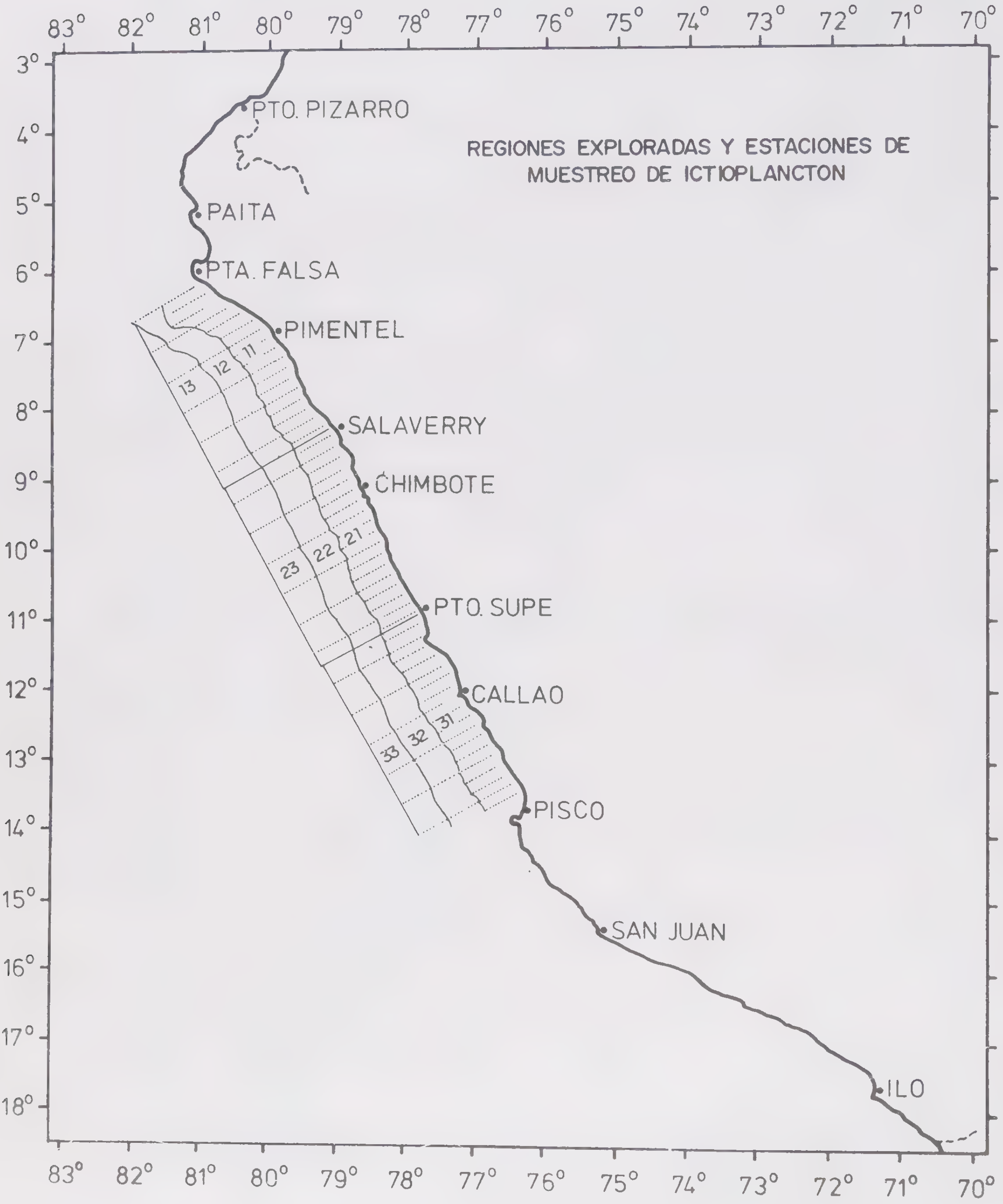
Fig. 2. Línea costera del Perú y estaciones de muestreo de anchoveta.


REGIONES EXPLORADAS Y ESTACIONES DE MUESTREO DE ICTIOPLANCTON
PTO. PIZARRO
PAITA
PTA. FALSA
PIMENTEL
SALAVERRY
CHIMBOTE
PTO. SUPE
CALLAO
PISCO
SAN JUAN
ILO
11
12
13
21
22
23
31
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33
83°
82°
81°
80°
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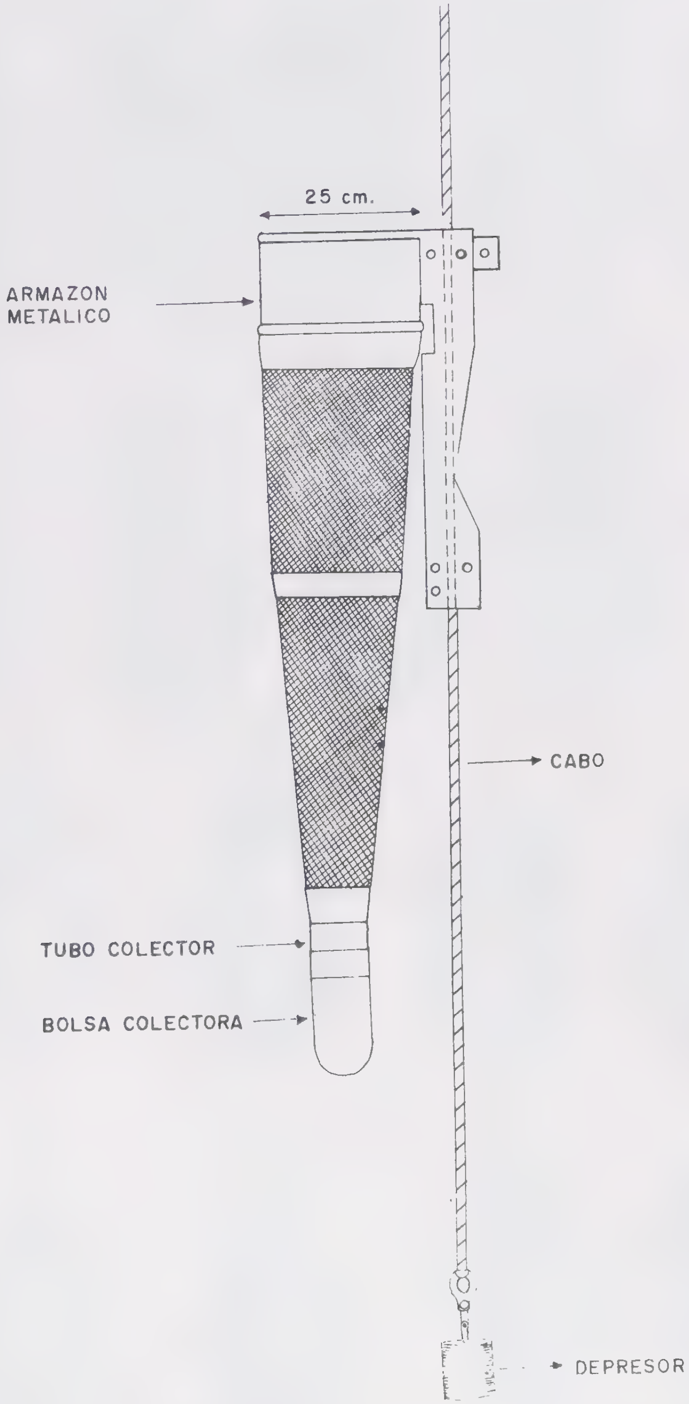
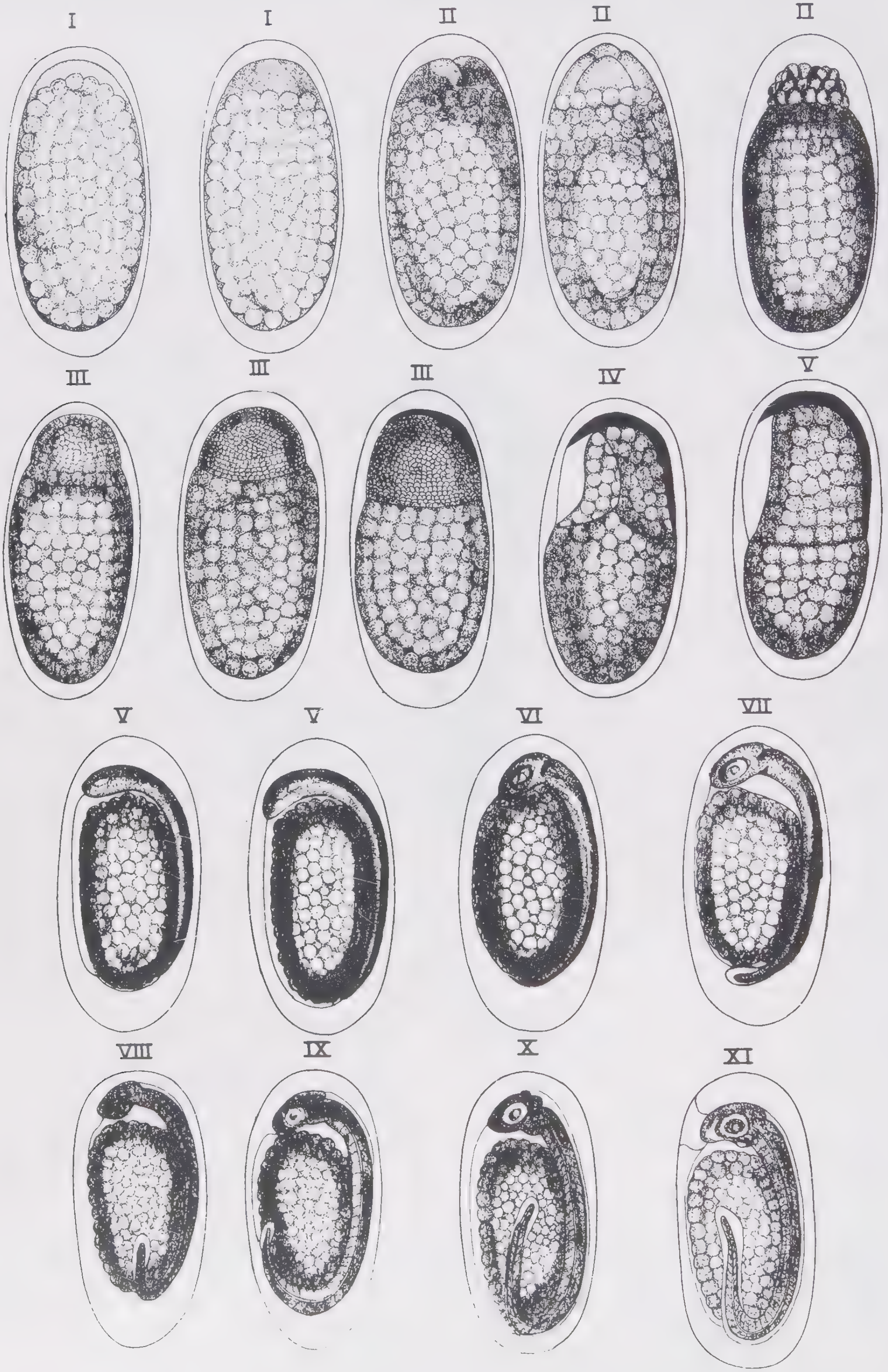
18°

Fig. 3. Línea Costera del Perú y estaciones de muestreo de ictioplancton.


25 cm.
ARMAZON METALICO
CABO
TUBO COLECTOR
BOLSA COLECTORA
DEPRESOR

[illegible] 4. [illegible] muestreo de huevos de [illegible]


I
I
II
II
II
III
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V
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V
VI
VII
VIII
IX
X
XI

Fig. 5. Desarrollo embrionario de anchoveta.

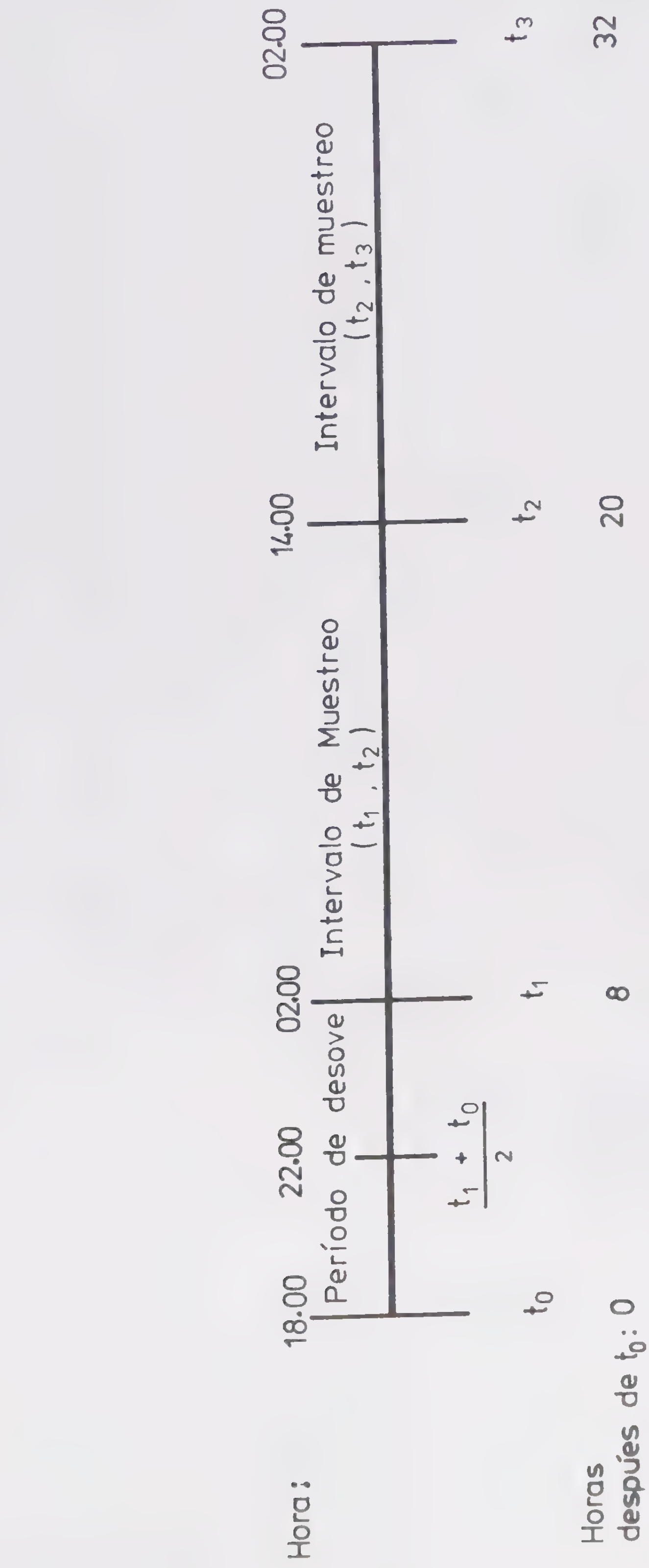
Hora :
18.00
22.00
02.00
14.00
02.00
Período de desove
Intervalo de Muestreo
(t1 , t2)
Intervalo de muestreo
(t2 , t3)
t0
$\frac{t_1 + t_0}{2}$
t1
t2
t3
Horas después de t0 : 0
8
20
32

Fig. 6. Representación esquemática de t_i.

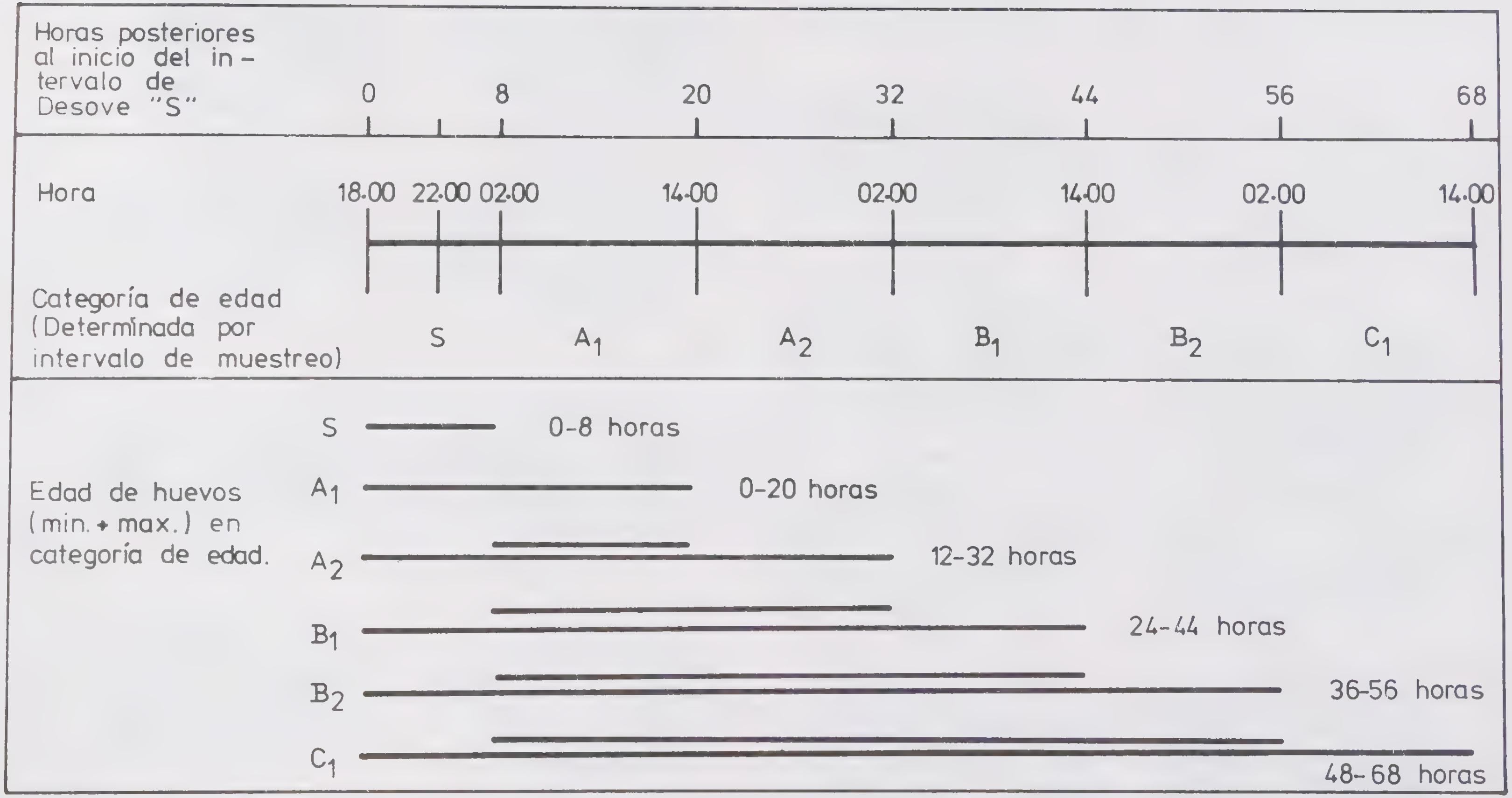
Horas posteriores al inicio del intervalo de Desove "S"
0
8
20
32
44
56
68
Hora
18.00
22.00
02.00
14.00
02.00
14.00
02.00
14.00
Categoría de edad (Determinada por intervalo de muestreo)
S
A1
A2
B1
B2
C1
Edad de huevos (min. + max.) en categoría de edad.
S
0-8 horas
A1
0-20 horas
A2
12-32 horas
B1
24-44 horas
B2
36-56 horas
C1
48-68 horas

Fig. 7. Representación esquemática de categorías de edad y edad máxima de huevos en diferentes categorías de edad.

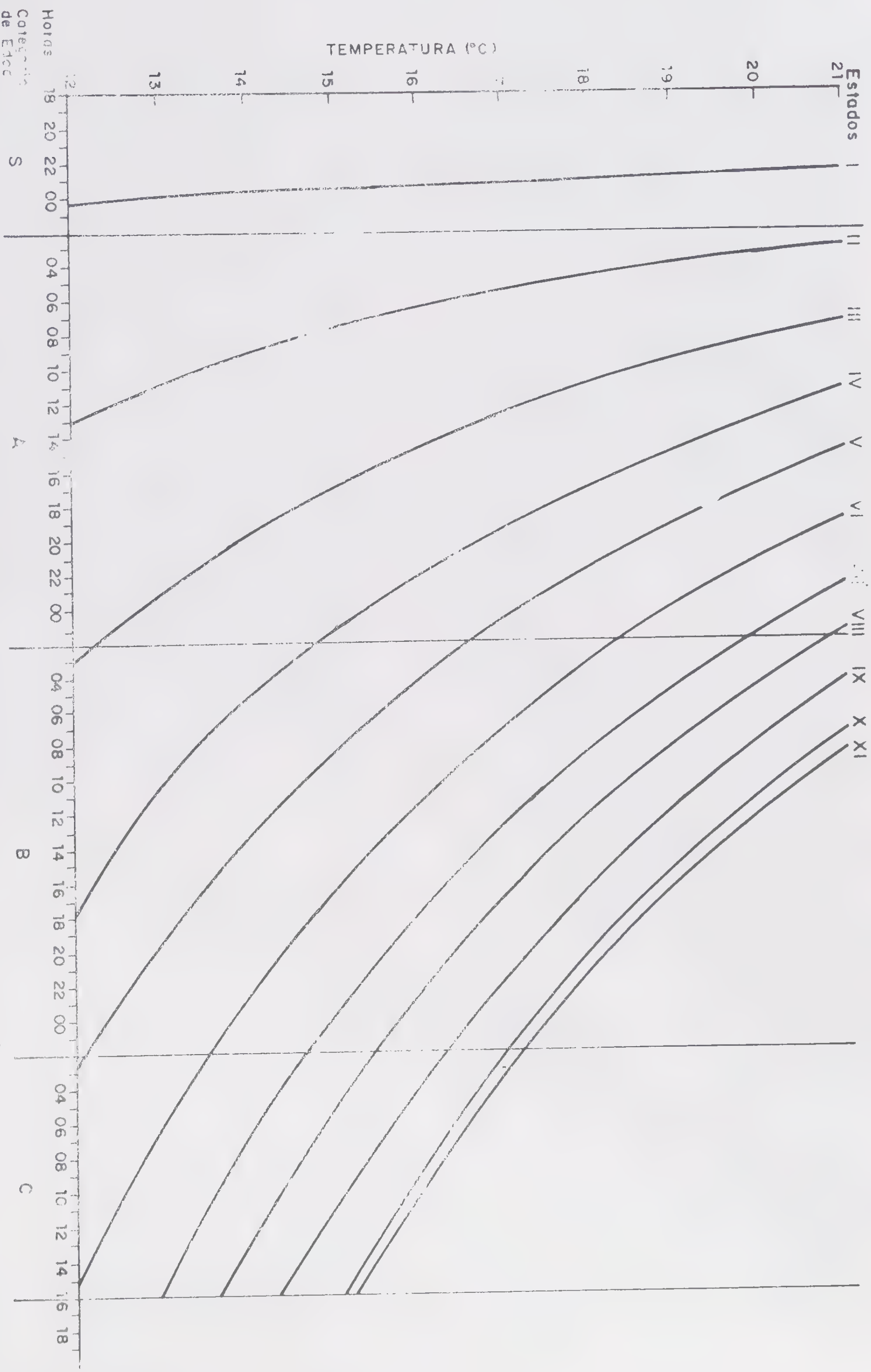

Figura 8. Curvas de desarrollo embrionario de anchoveta, que representan la edad de los estadios (I a XI) a diferentes temperaturas del agua.

```
200 DIM X#(20),Y#(20)
210 INPUT"NO.VAL.";N
220 FOR I=1 TO N
225 INPUT "T = ";X#(I)
230 INPUT "N = ";Y#(I)
235 PRINT
240 NEXT I
250 INPUT "REL.INTERVAL/TIME UNIT";B#
260 PRINT
270 INPUT "INIT. Z";Z#
280 GOSUB 500
290 F#=Z#*.1
300 S0#=S#
310 Z#=Z#+F#
320 PRINTZ#,S#
330 GOSUB 500
335 IF ABS (S0#/S#-1)< 1E -5 THEN 370
340 IF S#<S0# THEN 300
350 F#=F#/-2
360 GOTO 300
370 N0#=S2#/S3#
380 DT#=-LOG((1-EXP(-Z#*B#))/Z#/B#)/Z#
390 N0#=N0#*EXP(-Z#*-DT#)
400 '*************************** CALCULATE ERROR
401 M1#=0
402 M2#=0
403 M4#=0
410 FOR I=1 TO N
420 W1#=EXP((X#(I)+DT#)*-Z#
430 W2#=(X#(I)+DT#)*N0#*W1#
440 M1#=M1#+W1#[2
450 M2#=M2#+W1#*W2#
460 M4#=M4#+W2#[2
470 NEXT I
482 D#=M1#*M4#-M2#[2
484 C1#=M4#/D#
485 C2#=-M2#/D#
486 C4#=M1#/D#
488 E1#=SQR(C1#*S#/(N-2))
490 E2#=SQR(C4#*S#/(N-2))
491 PRINT:PRINT:PRINT
492 PRINT "N0= ";N0#,"ERROR = ";E1#
494 PRINT " Z= ";Z#,"ERROR = ";E2#
496 GOTO 590
500 ' ******************************SUBROUTINE FOR CALCULATING DEV
505 S1#=0
506 S2#=0
507 S3#=0
510 FOR I=1 TO N
520 S1#=S1# + Y#(I)[2
530 X0#=EXP(-Z#*X#(I))
540 S2#=S2# + Y#(I)*X0#
550 S3#=S3#.+ X0#[2
560 NEXT I
570 S#=(S1#-S2#[2/S3#)
580 RETURN
590 END
```

NOTES

MARKING GROWTH INCREMENTS IN OTOLITHS OF LARVAL AND JUVENILE FISH BY IMMERSION IN TETRACYCLINE TO EXAMINE THE RATE OF INCREMENT FORMATION

Age determination of fishes by counting daily growth increments in their otoliths is becoming a widely used technique in growth and population studies. Daily formation of otolith increments was first reported by Pannella (1971) for three species of temperate fish. Since then a number of workers, using three basic techniques for confirming the periodicity of increment formation, have reported the presence of daily increments in larval or adult otoliths of at least 15 species of marine and freshwater fishes. Laboratory rearing from eggs to larvae of known age was used to confirm daily increments by brothers et al. (1976), Taubert and Coble (1977), Barkman (1978), Tanaka et al. (1981), and Laroche et al. (1982). The change in the mean number of increments over time in fish captured in the wild and held in captivity was used to validate daily increments by Struhsaker and Uchiyama (1976), Wilson and Larkin (1980), and Uchiyama and Struhsaker (1981). The third method makes use of chemical agents to mark the growing margin of calcified structures in order to examine their rate of growth (Harris 1960). Tetracycline is one of the best chemical markers because it is relatively nontoxic and produces a fluorescent mark which is easily viewed in ultraviolet light (Harris 1960; Weber and Ridgway 1962). It has been administered to fish by feeding (Choate 1964; Weber and Ridgway 1967; Trojnar 1973; Odense and Logan 1974) and by injection (Kobayashi et al. 1964 and others below). Tetracycline has been used in two studies to determine the rate of increment formation in otoliths. Wild and Foreman (1980) injected the drug into large juveniles and adult skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in a mark-recapture program in the tropical eastern Pacific. They found that otoliths of yellowfin tuna of 40-110 cm FL showed daily average increment formation, but that skipjack tuna of 42-64 cm FL showed <1 increment/d. Campana and Neilson (1982) injected tetracycline into juvenile starry flounders, *Platichthys stellatus*, and found that daily increments were subsequently produced in both field and laboratory conditions. These authors briefly mentioned obtaining similar marking results by immersion, but did not detail their procedure.

This paper presents a technique for marking otolith increments by immersing larval and juvenile fish in a solution of tetracycline in seawater, and reports the rate of increment formation under laboratory conditions for two species from the Great Barrier Reef, Australia: *Hypoatherina tropicalis* (Altherinidae) and *Spratelloides dellicatulus* (Dussumeriidae).

Materials and Methods

The experiments were conducted between July 1980 and February 1982 at One Tree Island Field Station and Lizard Island Research Station, during a field study of the population dynamics of these species.

Achromycin (a brand of tetracycline HCl[1]) was used in all experiments. The concentration that would mark the otoliths but not kill the fish was determined by testing three concentrations (400 mg/l, 250 mg/l, and 40 mg/l) using *H. tropicalis* from 12.8 to 23.0 mm SL. The otoliths of survivors were compared with untreated specimens to assess the effectiveness of the mark.

The appropriate concentration, 250 mg/l, was then used in a series of similar experiments to determine the rate of increment formation (Table 1). The experiment number (I-IV) designates a group of fish collected at the same time. In each experiment, fish were killed at two different times, designated as A or B, to compare the number of increments in fish held for different time periods. In experiment IV, the treatment times also differed, but in all other experiments the treatment time was the same for both groups A and B.

Both species are small (adults <7 cm SL), midwater, reef-associated, schooling fishes which do not undergo a marked metamorphosis between larval and juvenile stages (pers. observ.). Both attain their full complement of fin elements and begin to form scales and adult pigmentation at a standard length of 17-19 mm. Following the convention of Ahlstrom (1968), I consider this to be the size at which larvae become juveniles. *Hypoatherina tropicalis* used in the rate-determination experiments ranged from 12.8 to 27.2 mm SL, with 10 of 21 fish classed as larvae (<17.0 mm SL). *Spratelloides delicatulus* ranged from 15.5 to 22.9 mm SL, with 2 of 29 being larvae (Table 1).

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[1] Manufactured by Lederle Labs, a division of Cyanamid Australia Pty. Ltd. References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

The fish were collected at night with a light and a dip net, and placed in 25 l aquaria without aeration or running seawater as soon as possible after collection. The aquaria were located outdoors under an awning, and therefore were exposed to the ambient diel light cycle, but not to direct sunlight. The fish were allowed to acclimatize for 12-24 h before treatment. Usually there was mortality during this period, but the proportion was not determined. All dead fish were removed prior to treatment.

The fish were exposed to 250 mg tetracycline/l seawater for 12 h from sunset to sunrise, except in experiment IVB when the immersion period was from sunrise to sunset (Table 1). After an immersion period, the aquarium was flushed with 90% water changes until no visible color remained. The tetracycline-seawater solution is yellow until exposed to sunlight for more than ~ 3 h, when it turns pink, due to oxidative photolysis. Following the treatment, fish were maintained in clean seawater for 2-6 d by feeding either fresh wild plankton >125 mm diameter once a day (experiment I) or *Artemia salina* nauplii 3-4 times/d (all subsequent experiments). *Artemia* nauplii were more convenient for frequent feedings than fresh wild plankton. Ninety percent of the water in each aquarium was changed each morning by siphoning, to minimize handling the fish. Tank water temperatures were measured over the diel cycle during February 1982 (summer) at One Tree Island. The temperature ranged from 25°C at 0630 h to 30°C at 1800 h. Replacement water, added at 0700 h from the surface of the lagoon, measured 27°C.

Larvae were killed at the end of each experiment by placing them into 70% ethanol. Fish were subsequently measured to the nearest 0.1 mm SL. Their otoliths (both sagittae and lapilli) were removed and mounted whole on glass slides without coverslips, using Protexx.

The following terms are used in this report for the concentric rings seen in otoliths. A growth zone is a wide ring which appears light or hyaline under transmitted light. A discontinuous zone is the narrower ring between two growth zones, often called the opaque zone because it appears dark under transmitted light. A growth increment, or simply an increment, is a growth zone plus a discontinuous zone.

Otoliths were examined at 250-1,000× magnification with a combination of incident ultraviolet light to reveal the fluorescent tetracycline-marked rings, and polarized transmitted light to count the rings. The fluorescence microscope used ultraviolet light from a 50W mercury lamp. Excitation wavelength was limited by a band pass filter (450-490 nm) and a long pass suppression filter (515 nm).

In most cases, one sagitta from each fish was read, although occasionally the lapillus was used if its rings were clearer. The area to be counted was selected by scanning the margin of each otolith to find the place where the greatest number of distinct rings could be seen between the innermost fluorescent increment and the edge. A datum was considered valid only if identical counts were obtained in at least two out of three blind readings. No other otoliths were considered in the analysis. Of 21 *H. tropicalis* otoliths

TABLE 1.—Summary of tetracycline-marking experiments to determine the rate of increment formation in *H. tropicalis* and *S. delicatulus*

Experiment	*N*	Standard length (mm) Mean (range)	Treatment period	Date and time of killing	Predicted no of discontinuous zones	No of fish with various deviations from the predicted number		
						−1	0	+1
Hypoatherina tropicalis								
IA	2(1)	14.0 (13.6-14.4)	2130, 8 July to 0830, 9 July 1980	0830, 12 July	2+1		1	1
IB	4	13.7 (12.8-14.7)	2130, 8 July to 0830, 9 July 1980	1730, 14 July	5		2	2
IIA	6([2]1)	20.5 (16.2-27.2)	1830, 31 Oct. to 0630, 1 Nov 1980	0730, 6 Nov.	4+1		5	
IIB	6	18.9 (16.8-20.7)	1830, 31 Oct. to 0630, 1 Nov. 1980	0600, 7 Nov.	5+1		6	
IIIA	3	16 1 (15.4-17.2)	2000, 6 Nov. to 0700, 7 Nov 1981	0545, 12 Nov.	4+1		3	
Total	21([2]1)					0	17	3
Spratelloides delicatulus								
IIIA	6	17.5 (15 5-19.1)	2000, 6 Nov. to 0700, 7 Nov. 1981	0545, 12 Nov.	4+1		3	3
IIIB	5([2]2)	17.9 (17.6-18.2)	2000, 6 Nov. to 0700, 7 Nov. 1981	1800, 9 Nov.	2			3
IVA	9	19.9 (18.8-22 8)	1800, 31 Jan to 0630, 1 Feb. 1982	1800, 6 Feb.	5	5	3	1
IVB	9([2]1)	20 5 (17 9-22.9)	0600 to 1800 31 Jun. 1982	0715, 6 Feb.	4+1	2	6	
Total	29([2]3)					7	12	7

[1] Otoliths of two treated fish were destroyed by poor preservation

[2] Number of fish discarded because of inconsistency between otolith readings

examined, 1 (4.8%) was discarded. Of 29 *S. delicatulus*, 3 (10.3%) were discarded (Table 1).

Results and Discussion

Marking Technique

In the experiment to determine an effective tetracycline-marking concentration, all fish ($n = 17$) in 400 mg/l died during the 12-h immersion period. Of 10 fish treated with 250 mg/l, 1 died during treatment, and 1 died during the subsequent holding period. Of 10 fish treated with 50 mg/l, 1 died during treatment.

Otoliths of untreated specimens showed faint fluorescence around the edge and occasionally along cracks and surface irregularities (Fig. 1A); this is a naturally occurring autofluorescence (Campana and Neilson 1982). Otoliths of fish in 50 mg/l were indistinguishable from those of untreated specimens. Otoliths of fish in 250 mg/l showed a strong fluorescent band medial to the edge, in addition to the weak fluorescence at the edge (Fig. 1B, C). This strong band consisted of two growth zones and one discontinuous zone (Fig. 2).

It is not known how long it takes for tetracycline to be incorporated into the growing otoliths when administered by immersion. Campana and Neilson (1982) reported that after injection, 50% of fish showed fluorescent otoliths after 10 h, and 100% after 24 h. If one assumes similar or slightly longer incorporation times in the present study, then the inner fluorescent growth zone was probably formed the day after the immersion period. The subsequent discontinuous zone and growth zone were formed while there was residual tetracycline in the water or fish. Another possible explanation is that the appearance of fluorescence in two growth zones is an artifact of viewing whole otoliths.

The results of this experiment indicate that immersion in a concentration of 250 mg Achromycin/l of seawater for 12 h is adequate to mark one or more growth increments in *H. tropicalis* and *S. delicatulus* larvae and juveniles. The overall mortality rate in experiments I, II, and III (total $n = 37$), was 5.4% during treatment and 2.7% during the holding phase.

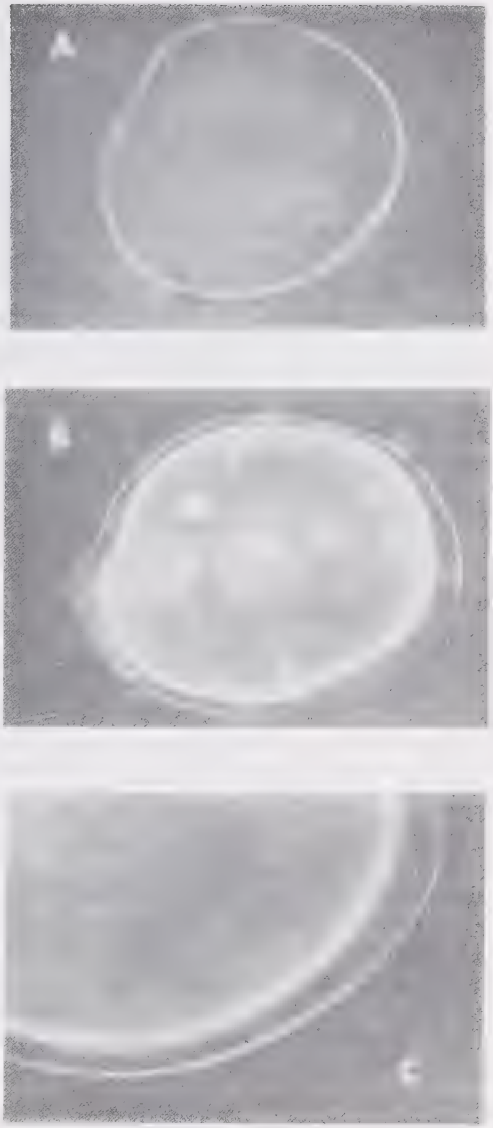

FIGURE 1.—Flourescence photomicrographs of sagittae of larval *Hypoatherina tropicalis*. A. Untreated otoliths, showing autofluorescence around the edge (10.1 mm SL). B. Tetracycline-marked otolith, showing fluorescent band medial to the edge (16.2 mm SL). C. Marked otolith under higher magnificaton (17.6 mm SL).

To determine whether fluorescent marking would occur if the tetracycline immersion period was during daylight hours, an experiment was conducted using *S. delicatulus* from 17.9 to 22.9 mm SL (experiment IV). The fish were collected and divided between two tanks. One tank received tetracycline from 1800 h to 0630 h, the other from 0600 to 1800 h. Mortality due to treatment was not monitored. After 6 d, the fish were killed and examined. The fluorescent bands medial to the edges were similar in width and intensity to those in previous experiments, and showed no difference between the two treatments. This indicates that tetracycline is incorporated into growing otoliths and produces fluorescent increments equally well during the day and night, regardless of whether the solution is yellow or has oxidized to pink.

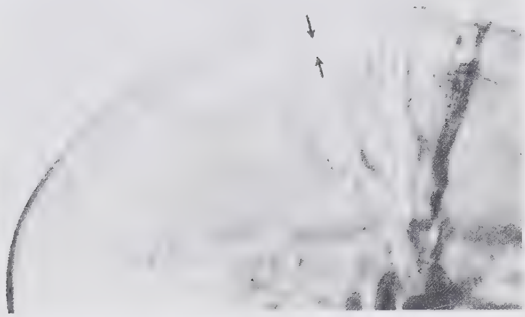

FIGURE 2.—Tetracycline-marked otolith from *H. tropicalis* (17.6 mm SL), photographed with a combination of fluorescent and transmitted polarized light. Arrows indicate the fluorescent band produced by the marking technique. This individual is from experiment IIB, and shows six discontinuous zones between the innermost fluorescent growth zone and the edge. The edge appears to be a growth zone.

In summary, tetracycline can be administered by three techniques: feeding, injection, and immersion. Feeding has apparently not been used in otolith studies. The immersion technique presented here has advantages over injection in some situations. It can be used on fish which are too small or fragile for injection. The fluorescent mark obtained is relatively narrow, covering only two increments, compared with the wider mark resulting from injection (Kobayashi et al. 1964; Campana and Neilson 1982). Therefore, it is distinguishable from edge autofluorescence after a shorter period of time, and allows finer resolution of increment formation, which may be useful in some experimental situations. Also, immersion requires minimum equipment, facilities, and handling of fish.

Rate of Increment Formation

In interpreting the results of my experiments, the number of discontinuous zones between the innermost fluorescent growth zone and the edge was compared with the number predicted if one discontinuous zone formed every day from ca. 0700 to 1000 h. Tanaka et al. (1981) found that growth zones in juvenile *Tilapia nilotica* held under various photoperiods started forming a few hours after lights-on, continued through the dark period, and stopped or slowed down about the time of the following lights-on. The discontinuous zone was formed in the few hours after lights-on. Mugiya et al. (1981) demonstrated that the deposition of calcium in goldfish, *Carassius auratus*, slowed down or stopped at sunrise and resumed in 3 h. Since otoliths are made of a matrix of organic fibers, which are calcified in the growth zones and not calcified in the discontinuous zones (Panella 1980; Watabe et al. 1982), the findings of Mugiya et al. (1981) support Tanaka et al. (1981). Whether this rhythm of increment formation is found in most fish remains to be investigated.

The results for all experiments are presented in Table 1. For fish that were killed between 0545 and 0830 h, the predicted number includes an additional discontinuous zone that should have been forming at the time of death, although this ring was probably not always sufficiently formed to be counted. In these cases, an otolith was considered to show daily increment formation even if the number of discontinuous zones was one less than predicted.

One growth increment was formed each day in 85% of *H. tropicalis* ($n = 20$); the rest had one more than the predicted number of increments. In *S. delicatulus*, 46% ($n = 26$) showed daily formation of growth increments; 27% showed one less, and 27% showed one more, than expected if increments form daily. Thus, the variability in rate of increment formation was greater in *S. delicatulus* than in *H. tropicalis*, but the average rate for *S. delicatulus* was still 1 increment/d.

This apparent difference in the rate of increment formation between species may be partially due to a difference between larvae and juveniles. Almost all (93%) of the *S. delicatulus* treated were juveniles, but only about half (52%) of the *H. tropicalis* were juveniles. However, no conclusion can be drawn from these data because the experiments were not designed to examine this factor, and the numbers are too small to compare larvae with juveniles.

It is possible that tetracycline may affect the rate of increment formation. Some workers have reported that tetracycline inhibits mineralization in scales and bone (Harris 1960; Kobayashi et al. 1964), although others note neither growth promotion, retardation, nor structural weakness in bone as a result of tetracycline administration (Weber and Ridgway 1967). The possibility that the tetracycline treatment interferes with growth of otoliths or fish was not considered in this study, but should be examined before further use is made of this technique.

In conclusion, the rate of increment formation has been examined in only a small number of species under a limited range of conditions. Recent evidence suggests that increment formation may be affected in some species by temperature, food availability and feeding frequency, photoperiod, and developmental stage (Taubert and Coble 1976; Brothers 1978; Pannella 1980; Wild and Foreman 1980; Geffen 1982;

Lough et al. 1982; Neilson and Geen 1982). It is therefore desirable to examine the rate of increment formation under various conditions before using otoliths for age determination (Brothers 1979). The technique presented here is a tool for studying increment formation in otoliths of young fish under laboratory and possibly field conditions. It can be used for reef and nearshore benthic species which can be captured while larvae or juveniles and kept in containers or enclosures.

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THE FOOD AND FEEDING HABITS OF THE GROUPER, EPINEPHELUS QUERNUS SEALE 1901, IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Sixty-seven stomach and spew samples of the grouper, *Epinephelus quernus*, from the Northwestern Hawaiian Islands were examined. The study showed that this grouper forages mainly on bottom-associated crustaceans, fishes, and cephalopods.

Shrimp (predominantly of the family Pandalidae) were the most important food item as determined by an index of relative importance (IRI). The IRI incorporates numbers and volumes of the prey and their frequency of occurrence. Of the 22 families of fishes that were represented in the food samples, members of the families Lutjanidae, Emmelichthyidae, and Congridae were the most important. The results suggest that *E. quernus* is a carnivorous, opportunistic bottom feeder.

Epinephelus quernus
Northwestern Hawaiian Islands
feeding

INTRODUCTION

Some of the Hawaiian fishes of highest commercial value are the bottomfishes which comprise the tropical snapper-grouper complex (Uchida et al., 1979). The lone serranid of commercial value within this group is the grouper, *Epinephelus quernus* Seale. Although the maximum size of this species is not known, specimens >105.9 cm total length and weighing 26.5 kg were caught on the resource survey cruises in the Northwestern Hawaiian Islands (NWHI) conducted by the Honolulu Laboratory, National Marine Fisheries Service (NMFS)(Uchida and Uchiyama, in preparation). This species is only recorded from Hawaii and is the only serranid which "contributes significantly to the commercial landings in Hawaii" (Tinker, 1978; Department of Land and Natural Resources, 1979).

The feeding studies on *Epinephelus* thus far have focused upon such species as *E. striatus*, *E. guttatus*, and *E. morio* in the Atlantic (Longley and Hildebrand, 1941; Bardach and Mowbray, 1955; Randall, 1965, 1967; Moe, 1969; Collette and Talbot, 1972) and *E. fuscoguttatus*, *E. merra*, and *E. hexagonatus* in the Indo-Pacific (Hiatt and Strasburg, 1960; Randall and Brock, 1960; Helfrich et al., 1968; Harmelin-Vivien and Bouchon, 1976; Randall, 1980). In general, these groupers are benthic carnivores and primarily feed on fishes and crustaceans. In addition, Randall (1965, 1967), Moe (1969), and Harmelin-Vivien and Bouchon (1976) found that groupers become more piscivorous as they increase in size.

Feeding periodicity of the groupers vary according to the geographical area and the species. Off Florida, *E. morio* feeds indifferently by day or night and *E. striatus* is primarily a diurnal feeder (Longley and Hildebrand, 1941). Serranids in the Caribbean Sea feed day and night and increase foraging activity during the crepuscular periods (Randall, 1967). Serranids in Madagascar also feed during day and night, but more actively at night (Harmelin-Vivien and Bouchon, 1976). In Tahitian waters, groupers are primarily diurnal; however, they may occasionally feed at night, especially in the presence of a bright moon (Randall and Brock, 1960).

These earlier studies have concentrated on groupers captured in nearshore waters. Although *E. quernus* may be found in the shallow, nearshore waters (Hobson, 1980), the food samples for this study were collected from fish captured on the offshore benthic slopes at depths of 128 to 219 m (70 to 120 fathoms).

Kluegel (1921) published the only report on the feeding habits of *E. quernus*. In her study of the diet of food fishes, she found that this grouper was carnivorous. This was based on the contents of 13 stomachs (10 of which were empty) and the presence of scombroid fish among the food items.

The major objective of this study is to quantitatively determine specific forage items of this deep-dwelling species. This study was part of an overall investigation of the life history of this species and other bottomfishes. Together with feeding studies of other species, such as *Pseudocaranx dentex* (see report in this proceedings by Michael P. Seki), occupying the same or comparable habitat, this diet study of the grouper may provide data on competition among species for prey, and thus may lead to a better understanding of trophic relationships.

METHODS

Field Collection of Food Samples

The 67 stomach and spew samples were collected from groupers captured at deep-sea handlining stations aboard cruises to the NWHI from March 1978 to August 1981. Fifty-nine of the samples were collected on the RV Townsend Cromwell, whereas four spew samples each were collected aboard commercial vessels, the FV Easy Rider, and the FV Libra.

The fish (34 females, 2 males, and 31 unsexed) were captured at 21 islands or banks stretching from Nihoa to Kure Atoll. They ranged from 38.7 to 109.3 cm total length and weighed from 1.8 to 22.7 kg. The study material included 14 stomachs removed intact from the fish and 53 spew samples.

The handlined fish were caught primarily on hydraulic-powered gurdies, although a few fish from early cruises may have been hauled by hand or on an electric reel. The terminal rig and gurdy specifications are reported by Uchida and Uchiyama (in preparation). Most of the grouper landed were caught on rigs with four hook lines and Tankichi or Izuo ulua hooks Nos. 26 and 28 baited with stripped squid. At handline stations, the vessel was usually allowed to drift over banks 73 to 219 m (40 to 120 fathoms) deep.

Since the fish were taken from great depths, most of the stomachs were everted due to gas bladder expansion when the fish were brought to the surface and much of the contents were regurgitated. Many food items, however, were caught in the throat or gill rakers and were picked out by long forceps and saved. These were classified as spews. All stomachs and spews were preserved immediately in a 10 percent Formalin-seawater mixture. Data on species, station number, date of capture, total and standard lengths, weight, and sex were noted for each sample.

Laboratory Procedure

The laboratory methods for examination of the samples were similar to those reported in Humphreys (1980) and Harrison et al. (1983). For this study, the analyses of stomach and spew samples were treated similarly. The stomach contents were emptied into a fine mesh strainer, rinsed in running water, and sorted into identifiable groups. The volume of the prey items were measured by water displacement and coded for stage of digestion. The codes ranged from 1 through 4 where code 1 represented an item with no perceptible loss in volume and code 4 an item almost completely digested. When more than one item in the same taxon were present and could not be distinguished as whole individual items, the total number and volume of the items were recorded.

Where possible, lengths of the prey items were determined. The measurements, which included standard length (SL) for fish, mantle length (ML) for cephalopods, and carapace length (CL) for crustaceans, were coded as follows: code 1, totally intact specimen which could be measured precisely, and code 2, inexact measurement of a partially digested specimen. No attempt was made to measure the length of any prey item that was well digested.

Food items were identified to the lowest taxon possible, using the methods reported in Harrison et al. (1983). To identify fish, external characteristics and morphometrics were used whenever possible; however, many fish were in an advanced state of digestion and required clearing and staining in Alizarin S so that vertebral counts and morphological characters could be used for identification purposes. Invertebrates were identified by external morphological features. Thus, many of the crustaceans were identified at least to family since the exoskeletons remained intact despite digestion.

Method of Data Analysis

Traditionally, numerical, volumetric, and frequency of occurrence methods have been used in expressing results of food studies. Reintjes and King (1953) stated that, individually, each method has shortcomings, but food items which ranked high in number, volume, and frequency of occurrence were important foods for the predator at the time and area sampled.

Pinkas et al. (1971) attempted to incorporate the three traditional methods of stomach analysis in the development of an index of relative importance (IRI) expressed as:

$$IRI = (N+V)F$$

where

N = percentage of the total number of prey items
V = percentage of the total aggregate volume of the prey items
F = percentage of the occurrence in the stomach samples

For this study, the importance of each of the forage items was determined by the IRI method. The number, volume, and frequency of occurrence percentages were rounded off to the nearest 10th prior to the IRI calculations.

RESULTS

A list of the food items in the 67 stomach and spew samples is presented in Table 1. The numerical, volumetric, and frequency of occurrence analyses, along with the IRI values, are given for the forage items identified to the lowest taxon.

TABLE 1. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME AND INDEX OF RELATIVE IMPORTANCE (IRI) OF THE FORAGE ITEMS IN 67 *EPINEPHELUS QUERNUS* FOOD SAMPLES

Forage Items	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
PHYLUM MOLLUSCA							
Class Cephalopoda	1	0.2	11	1.5	23.0	0.7	1.4
Order Octopoda	4	0.8	3	4.5	239.0	7.6	37.8
PHYLUM ARTHROPODA							
Class Crustacea							
Subclass Malacostraca							
Order Isopoda	1	0.2	1	1.5	0.6	<0.1	0.3
Order Amphipoda							
Family Phronimidae							
Phronima sedentaria	1	0.2	1	1.5	1.0	<0.1	0.3
Order Stomatopoda							
Family Squillidae							
Odontodactylus brevirostris	1	0.2	1	1.5	6.5	0.2	0.6
Order Decapoda							
Suborder Natantia (shrimp)	56	11.5	9	13.4	43.6	1.4	172.9
Superfamily Caridea	27	5.6	5	7.5	17.6	0.6	46.5
Family Pandalidae	308	63.4	16	23.9	212.7	6.8	1,677.8
Plesionika longirostris	5	1.0	2	3.0	14.5	0.5	4.5
"Shrimp remains"	—	—	1	1.5	0.3	<0.1	—
Suborder Reptantia	2	0.4	2	3.0	9.8	0.3	2.1
Tribe Anomura							
Family Galatheidae	1	0.2	1	1.5	2.0	0.1	0.4
Munida sp.	2	0.4	2	3.0	3.5	0.1	1.5
Tribe Brachyura	3	0.6	2	3.0	101.0	3.2	11.4
Family Homolidae	1	0.2	1	1.5	20.0	0.6	1.2
Family Raninidae	1	0.2	1	1.5	27.0	0.9	1.6
PHYLUM ECHINODERMATA							
Class Echinoidea	1	0.2	1	1.5	0.3	<0.1	0.3
PHYLUM CHORDATA							
Subphylum Tunicata							
Family Pyrosomatidae	1	0.2	1	1.5	23.0	0.7	1.4
Superclass Pisces							
Class Osteichthyes							
(unidentified fishes)	3	0.6	3	4.5	101.5	3.2	17.1
Order Anguilliformes	2	0.4	1	1.5	13.7	0.4	1.2
Family Congridae	5	1.0	4	6.0	307.0	9.8	64.8
Family Muraenidae	1	0.2	1	1.5	5.0	0.2	0.6
Order Salmoniformes							
Family Argentinidae	1	0.2	1	1.5	3.5	0.1	0.4

Note: Food items were identified to the lowest taxon possible

TABLE 1. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME AND INDEX OF RELATIVE IMPORTANCE (IRI) OF THE FORAGE ITEMS IN 67 *EPINEPHELUS QUERNUS* FOOD SAMPLES (continued)

Forage Items	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
Order Gonorhynchiformes							
Family Gonorhynchidae							
Gonorhynchus gonorhynchus	1	0.2	1	1.5	1.9	0.1	0.4
Order Myctophiformes							
Family Myctophidae	3	0.6	2	3.0	76.1	2.4	9.0
Order Polymixiiformes							
Family Polymixiidae	1	0.2	1	1.5	60.0	1.9	3.2
Polymixia berndti	1	0.2	1	1.5	14.0	0.4	0.9
Order Gadiformes							
Family Ophidiidae							
Brotula multibarbata	1	0.2	1	1.5	32.0	1.0	1.8
Order Beryciformes							
Family Trachichthyidae	2	0.4	2	3.0	2.3	0.1	1.5
Paratrachichthys sp.	3	0.6	2	3.0	13.5	0.4	3.0
Family Holocentridae	1	0.2	1	1.5	4.0	0.1	0.4
Order Scorpaeniformes							
Family Scorpaenidae	1	0.2	1	1.5	24.0	0.8	1.5
Order Perciformes							
Family Serranidae	4	0.8	3	4.5	130.5	4.2	22.5
Family Priacanthidae							
Priacanthus sp.	1	0.2	1	1.5	10.0	0.3	0.8
Family Apogonidae	2	0.4	1	1.5	1.5	<0.1	0.6
Family Echeneidae	4	0.8	4	6.0	307.0	9.8	63.6
Family Carangidae							
Decapterus sp.	1	0.2	1	1.5	1.8	0.1	0.4
Seriola sp.	1	0.2	1	1.5	24.0	0.8	1.5
Family Emmelichthyidae	15	3.1	8	11.9	176.4	5.6	103.5
Family Lutjanidae	1	0.2	1	1.5	136.0	4.3	6.8
Etelis carbunculus	1	0.2	1	1.5	780.0	24.8	37.5
Symphysanodon sp.	4	0.8	3	4.5	7.5	0.2	4.5
Family Mullidae							
Parupeneus sp.	1	0.2	1	1.5	43.0	1.4	2.4
Family Pomacentridae	1	0.2	1	1.5	10.0	0.3	0.8
Family Gempylidae	1	0.2	1	1.5	81.0	2.6	4.2
Order Tetraodontiformes							
Family Monacanthidae	1	0.2	1	1.5	5.5	0.2	0.6
Pervagor spilosoma	1	0.2	1	1.5	7.0	0.2	0.6
Family Tetraodontidae	1	0.2	1	1.5	2.5	0.1	0.4
Unidentified fish remains	—	—	2	3.0	13.7	0.4	—
OTHERS							
Unidentified remains	—	—	1	1.5	1.3	0.1	—
"Coral rubble"	—	—	1	1.5	3.5	<0.1	—

Table 2 presents the analysis of the food items by major classes and groups. The classes are listed in descending order of IRI values for fishes and invertebrates. Primarily, the prey fishes are presented by the families and the invertebrates by class or order. The IRI values and the percentages used in the IRI calculations are given in the table.

Overall, fishes (IRI = 5,384.9) and crustaceans (IRI = 5,009.2) made up the bulk of the forage items. Molluscs (IRI = 54.9), other miscellaneous invertebrates (IRI = 3.3), and unidentifiable remains made up the rest of the food items.

Fishes, representing 22 families, occurred in 59.7 percent of the food samples, comprised 76.2 percent of the total aggregate volume, and represented 14.0 percent of the total number of food items. Lutjanidae (229.5), Emmelichthyidae (103.5), and Congridae (64.8) had the highest IRI. Although unidentified fishes (IRI = 17.1) are significantly represented, the individuals represented various species.

Crustaceans, which made up the majority of the invertebrate forage, appeared in 50.7 percent of the samples and comprised 84.2 percent of the organisms and 14.6 percent of the total aggregate volume. Shrimp (Natantia) represented 96.8 percent of all the crustaceans, and the family Pandalidae represented 79.0 percent of all the shrimp. the lone species of shrimp identifiable beyond the family level was *Plesionika longirostris*. crabs (Reptantia), stomatopods, amphipods, and isopods made up the rest of the crustaceans in the forage.

Molluscs were present in 5.9 percent of the samples; all but one were octopuses. They comprised 8.3 percent of the total aggregate volume and 1.0 percent of the total number of forage items.

Other invertebrates were not significant contributors to the forage. One tunicate, family Pyrosomatidae, and an echinoid comprised 3.0 percent of the forage and made up 0.7 percent of the total aggregate volume and 0.4 percent of the organism total.

Unidentified remains and coral rubble comprised the remaining items in the samples. The IRI for these classifications and "fish remains" was not computed because it was not possible to determine the number of these items in the samples.

Individual lengths, length ranges, and mean lengths of the prey items are presented in Table 3. The lengths of prey fish ranged from 35 mm (a trachichthyid) to 516 mm (a congrid eel). Among the invertebrates, lengths ranged from 7-mm CL (a pandalid shrimp) to 85 mm ML (an octopod).

TABLE 2. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME, AND INDEX OF RELATIVE IMPORTANCE (IRI) FOR MAJOR CLASSES OF FORAGE ITEMS IN 67 *EPINEPHELUS QUERNUS* FOOD SAMPLES

Forage Classes	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
INVERTEBRATES							
Natantia (shrimp)	396	81.5	24	35.8	288.9	9.2	3,247.1
Reptantia	10	2.1	8	11.9	163.3	5.2	86.9
Cephalopoda	5	1.0	4	6.0	262.0	8.3	55.8
Tunicata	1	0.2	1	1.5	23.0	0.7	1.4
Stomatopoda	1	0.2	1	1.5	6.5	0.2	0.6
Amphipoda	1	0.2	1	1.5	1.0	<0.1	0.3
Isopoda	1	0.2	1	1.5	0.6	<0.1	0.3
Echinoidea	1	0.2	1	1.5	0.3	<0.1	0.3
FISHES							
Lutjanidae	6	1.2	5	7.5	923.5	29.4	229.5
Emmelichthyidae	15	3.1	8	11.9	176.4	5.6	103.5
Congridae	5	1.0	4	6.0	307.0	9.8	64.8
Echeneidae	4	0.8	4	6.0	307.0	9.8	63.6
Serranidae	4	0.8	3	4.5	130.5	4.2	22.5
Trachichthyidae	5	1.0	4	6.0	15.8	0.5	9.0
Myctophidae	3	0.6	2	3.0	76.1	2.4	9.0
Polymixiidae	2	0.4	2	3.0	74.0	2.4	8.4
Gempylidae	1	0.2	1	1.5	81.0	2.6	4.2
Carangidae	2	0.4	2	3.0	25.8	0.8	3.6
Monacanthidae	2	0.4	2	3.0	12.5	0.4	2.4
Mullidae	1	0.2	1	1.5	43.0	1.4	2.4
Ophidiidae	1	0.2	1	1.5	32.0	1.0	1.8
Scorpaenidae	1	0.2	1	1.5	24.0	0.8	1.5
Anguilliformes (unidentified eels)	2	0.4	1	1.5	13.7	0.4	1.2
Priacanthidae	1	0.2	1	1.5	10.0	0.3	0.8
Pomacentridae	1	0.2	1	1.5	10.0	0.3	0.8
Apogonidae	2	0.4	1	1.5	1.5	<0.1	0.6
Muraenidae	1	0.2	1	1.5	5.0	0.2	0.6
Holocentridae	1	0.2	1	1.5	4.0	0.1	0.4
Argentinidae	1	0.2	1	1.5	3.5	0.1	0.4
Tetraodontidae	1	0.2	1	1.5	2.5	0.1	0.4
Gonorhynchidae	1	0.2	1	1.5	1.9	0.1	0.4
Unidentified fishes	3	0.6	3	4.5	101.5	3.2	17.1
Fish remains	—	—	2	3.0	13.7	0.4	—
OTHERS							
Unidentified remains	—	—	1	1.5	1.3	0.1	—
"Coral rubble"	—	—	1	1.5	3.5	0.1	—

TABLE 3. LENGTHS AND LENGTH RANGES OF ITEMS FOUND IN 67 *EPINEPHELUS QUERNUS* FOOD SAMPLES

Forage Items	No. of Organisms	Lengths or Range of Length and Mean Length (mm)
INVERTEBRATES		
Cephalopoda		
Octopoda	2	47-85 ($\bar{x}$ = 66.0)
Crustaceans		
Isopoda	1	27
Stomatopoda		
Odontodactylus brevirostris	1	75
Decapoda		
Natantia (shrimp)	2	10-13 ($\bar{x}$ = 11.5)
Caridea	1	12
Pandalidae	98	7-20 ($\bar{x}$ = 11.35)
Plesionika longirostris	5	13-22 ($\bar{x}$ = 16.8)
Reptantia		
Galatheidae	1	45
Munida sp.	2	24-38 ($\bar{x}$ = 36.0)
Brachyura	3	38-39 ($\bar{x}$ = 38.33)
Homolidae	1	43
Raninidae	1	66
FISHES		
Anguilliformes		
(unidentified eels)	1	174
Congridae	4	116-516 ($\bar{x}$ = 297.75)
Argentinidae	1	79
Gonorhynchidae		
Gonorhynchus gonorhynchus	1	78
Myctophidae	2	146-156 ($\bar{x}$ = 151.0)
Polymixiidae	1	161
Polymixia berndti	1	87
Ophidiidae		
Brotula multibarbata	1	158
Trachichtyidae	2	35-37 ($\bar{x}$ = 36.0)
Paratrachichthys sp.	3	50-67 ($\bar{x}$ = 57.33)
Holocentridae	1	63
Serranidae	3	93-197 ($\bar{x}$ = 143.33)
Priacanthidae		
Priacanthus sp.	1	71
Echeneidae	4	179-197 ($\bar{x}$ = 237.5)
Carangidae		
Seriola sp.	1	125
Emmelichthyidae	9	45-126 ($\bar{x}$ = 96.89)

TABLE 3. LENGTHS AND LENGTH RANGES OF ITEMS FOUND IN 67 *EPINEPHELUS QUERNUS* FOOD SAMPLES (continued)

Forage Items	No. of Organisms	Lengths or Range of Length and Mean Length (mm)
Lutjanidae	1	202
Etelis carbunculus	1	377
Symphysanodon sp.	4	53-56 ($\bar{x}$ = 54.25)
Mullidae		
Parupeneus sp.	1	128
Pomacentridae	1	68
Gempylidae	1	267
Monacanthidae	1	67
Pervagor spilosoma	1	66

Note: Means are given in parentheses

DISCUSSION AND CONCLUSION

As mentioned earlier, most of the food samples were spews which were caught in the throat or gill rakers of the groupers when the stomachs everted due to gas bladder expansion. It is possible that the spewed organisms are more likely to be retained due to some morphological structure (such as the antennules and antennae of pandalid shrimps) or perhaps size, and therefore a biased interpretation of the actual feeding habits and diet may result. Thus, it is possible that the results obtained may not completely represent the diet of this species. This problem was also encountered by Kluegel (1921) in the deeper-dwelling food fishes (including *E. quernus*), by Forster et al. (1970) in *Etelis marshi* (= *E. carbunculus*, Anderson (1981)), and by Moe (1969) in the red grouper in the Gulf of Mexico.

The results of this study support the conclusions of other studies on *Epinephelus*, i.e., *E. quernus* is a benthic carnivore. This grouper appears to be primarily piscivorous, although crustaceans and cephalopods also contribute to the forage. As concluded with other species of *Epinephelus* (Bardach and Mowbray, 1955; Hiatt and Strasburg, 1960; Moe, 1969), *E. quernus* appears to be an unspecialized feeder.

The items found in the food samples reflect the bottom-feeding behavior of this grouper. All 22 of the identified fish families contributing to the diet are usually found near the bottom, most being bottom inhabitants. Of particular interest was the occurrence of a red snapper, *E. carbunculus* (377 mm for length), in the stomach of a large (1,059 mm total length) grouper. This snapper is also a bottomfish which belongs to the tropical snapper-grouper complex mentioned earlier.

The invertebrates in the diet were generally small; shrimp were numerous. Shrimp (primarily Pandalidae) appear to be a very important food item for this grouper in the NWHI. Again, it is possible that the abundance of shrimp in the forage may be attributed to the sampling problem and that the long appendages characteristic of the shrimp are responsible for their high representation in the diet. However, 120 shrimp were found in one intact stomach. The lone pandalid shrimp that was identifiable to species was _P_. _longirostris_. King (1981) showed that this species was distributed along the benthic slopes in tropical Pacific islands, and our trapping results show this to hold true in the NWHI. This would indicate that the shrimp occupy a similar habitat as _E_. _quernus_, and thus their presence in the diet is not surprising. The presence of other invertebrates such as octopuses and galatheid crabs among the forage items further show the opportunistic benthic foraging behavior of _E_. _quernus_ as well as a potential nocturnal or crepuscular behavior. Time of feeding, however, could not be determined due to lack of sufficient data. This species will take a baited hook both night and day (Moffitt, 1980), so it seems that _E_. _quernus_, like its congeners (Longley and Holdebrand, 1941; Randall and Brock, 1960; Randall, 1967; Harmelin-Vivien and Bouchon, 1976), feeds indifferently by day or night but may increase its foraging activities during certain periods of the day.

Trapping data collected on research cruises to the NWHI indicated possible depths of foraging by the grouper (Uchida and Uchiyama, in preparation). Adult _E_. _quernus_ were caught in depths ranging from 18 to 230 m (10 to 126 fathoms) which includes the depths over which bottom handlining stations were conducted. This suggests that the grouper may forage over a wide range of depths very close to the bottom.

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THE FOOD AND FEEDING HABITS OF THE WHITE TREVALLY, *PSEUDOCARANX DENTEX* (BLOCH AND SCHNEIDER 1801), IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Sixty-four stomach samples of the white trevally, *Psuedocaranx dentex*, caught in the Northwestern Hawaiian Islands were examined to quantitatively determine the items which comprise the diet of this commercially valuable food species.

The results indicated that the white trevally is an opportunistic carnivore. It is primarily piscivorous, although cephalopods and crustaceans are also major contributors to the diet. The findings also strongly indicate that white trevally feeds near the bottom in the deeper waters offshore.

An index of relative importance (IRI) was computed to indicate which forage items were most important to the predators sampled. The IRI incorporates the frequency of occurrence and the percentage in the number and volume of the prey. The IRI showed that members of the families Congridae, Priacanthidae, and Serranidae were the most important fish prey. Cephalopods, crabs, and shrimp had the highest IRI among the invertebrates.

Carangidae *Pseudocaranx dentex*
feeding Northwestern Hawaiian Islands

INTRODUCTION

A food study of commercially important bottomfishes was undertaken as part of a survey and assessment of the benthic slope resources in the Northwestern Hawaiian Islands (NWHI). Among the species that comprise these resources is the whit trevally, *Pseudocaranx dentex*, also known in Hawaii as the thick-lipped jack, butaguchi, or pig ulua. This species has been known as *Caranx cheilio* Snyder 1904; however, according to Smith-Vaniz and Poss (Department of Ichthyology, The Academy of Natural Sciences of Philadelphia, April, 1982: personal communication), who are working on a revision of the genus *Pseudocaranx*, *C. cheilio* is a synonym of *P. dentex* (Bloch and Schneider 1801). Around Hawaii the species attains a length of 91 cm (3 ft) (Gosline and Brock, 1960).

Outside the NWHI, the Indo-Pacific distribution of *P. dentex* includes South Africa, Australia, Tasmania, Norfolk Island, New Zealand, Japan, Pitcairn, Rapa, Easter, and the Lord Howe Islands (Randall, 1981). In the NWHI, the white trevally is found mainly on the banks and benthic slope at depths between 73 and 183 m (40 and 100 fathoms). The distribution of this species is not, however, limited to the deep slopes. At Kure Atoll, Okamoto and Kawamoto (1980) observed the white trevally in waters 1.5 m (5 ft) deep, occasionally in large schools of 200 to 300 individuals. Hobson (1980) found the species on his transect lines at Midway in depths of 5 m, and traps set as shallow as 18 m (10 fathoms) during our NWHI studies have captured both juveniles and adults.

Although feeding studies of *P. dentex* are nonexistent, a few feeding studies on other species of the family Carangidae have been published. Hobson (1974) and Okamoto and Kawamoto (1980) briefly mentioned the foraging habits of the bluefin trevally, *C. melampygus*, on Hawaiian inshore coral reefs. The same species has been studied on the reefs of the Gilbert Islands (Randall, 1955), the Marshall Islands (Hiatt and Strasburg, 1960; Randall, 1980), and off the east coast of Africa (Williams, 1965). The foraging habits of the giant trevally, *C. ignobilis*, were studied in the Marshall Islands (Randall, 1980), off East Africa (Williams, 1965), and in the NWHI (Okamoto and Kawamoto, 1980; Parrish et al., 1980). Feeding habits of various other common jacks, such as *C. lugubris*, have also been covered by Randall (1955, 1967, 1980). In general, the studies have found jacks to be primarily piscivores; however, the time of feeding appeared to vary among the species. *Caranx melampygus* is a diurnal predator (Williams, 1965; Okamoto and Kawamoto, 1980; Potts, 1980) whereas *C. ignobilis* is a nocturnal feeder (Okamoto and Kawamoto, 1980). In his examination of stomach contents from five species of *Caranx*, Randall (1967) noted that although some species were not ordinarily reef residents, many individuals made foraging trips into reef communities.

At the present time, the knowledge of the feeding habits of jacks has been limited to the species which may be easily captured on the nearshore reefs, although *C. ignobilis* may also be taken in waters as deep as 70 m (40 fathoms). *Pseudocaranx dentex* is known to inhabit coastal waters about 146 m (80 fathoms) deep with other commercially important food species such as the pink snapper or opakapaka, *Pristipomoides filamentosus*, and the hapuupuu, Epinephelus quernus (Hawaii Department of Land and Natural Resources, 1979; Ralston, 1981, 1982). The major objective of this study was to quantitatively determine the items constituting the diet of this deep-dwelling species. Together with food studies of other sympatric predators such as E. quernus (see paper on grouper in this proceedings by Seki), this study may provide a better understanding of the trophic relationships among the species of the demersal community in the NWHI.

METHODS

Field Collection of Food Samples

Sixty-four stomach samples of adult white trevally were collected at deep-sea handline stations aboard the RV Townsend Cromwell on resource survey cruises to the NWHI from September 1978 to August 1981. The samples were collected at 11 banks from Nihoa to Kure Atoll (Figure 1).

Fish sampled ranged from 42.7 to 82.2-cm fork length and weighed from 1.35 to 10.73 kg. Thirty-three of the specimens were females, 29 were males, and 2 were unsexed. Sixty of the samples were whole stomachs removed intact from the fish. The remaining four consisted of regurgitated food items removed from the gill rakers. Empty stomachs were not collected.

The fish were caught with hook and line on hydraulic-powered gurdies. The terminal rig and gurdy specifications have been described in a forthcoming publication edited by R.N. Uchida and J.H. Uchiyama. Briefly, the gurdies had a terminal rig with four hooks (Tankichi or Izuo No. 26 and/or No. 28). Each hook was usually baited with stripped squid. Handline stations were conducted with the vessel adrift in depths of 73 to 220 m (40 to 120 fathoms).

When fish were landed, stomachs were removed, examined, and unless empty, preserved in a 10 percent Formalin-seawater solution for later analysis. Regurgitated food items (spew) caught in the gill rakers when the stomachs everted due to gas bladder expansion were also preserved.

Laboratory Procedure

The laboratory methods for examination of the samples were similar to those reported by Humphreys (1980) and Harrison et al. (1983). The stomach contents were emptied into a fine mesh strainer, rinsed in running water, and sorted into identifiable groups. The volume of prey items were measured by water displacement. Where more than one item in the same taxon was present and could not be distinguished as a whole individual, the total volume and number of individuals comprising the volume were recorded. When possible, lengths of the prey were taken, including standard length for fish, mantle length for cephalopods, carapace length for shrimp, carapace width for crabs, and total

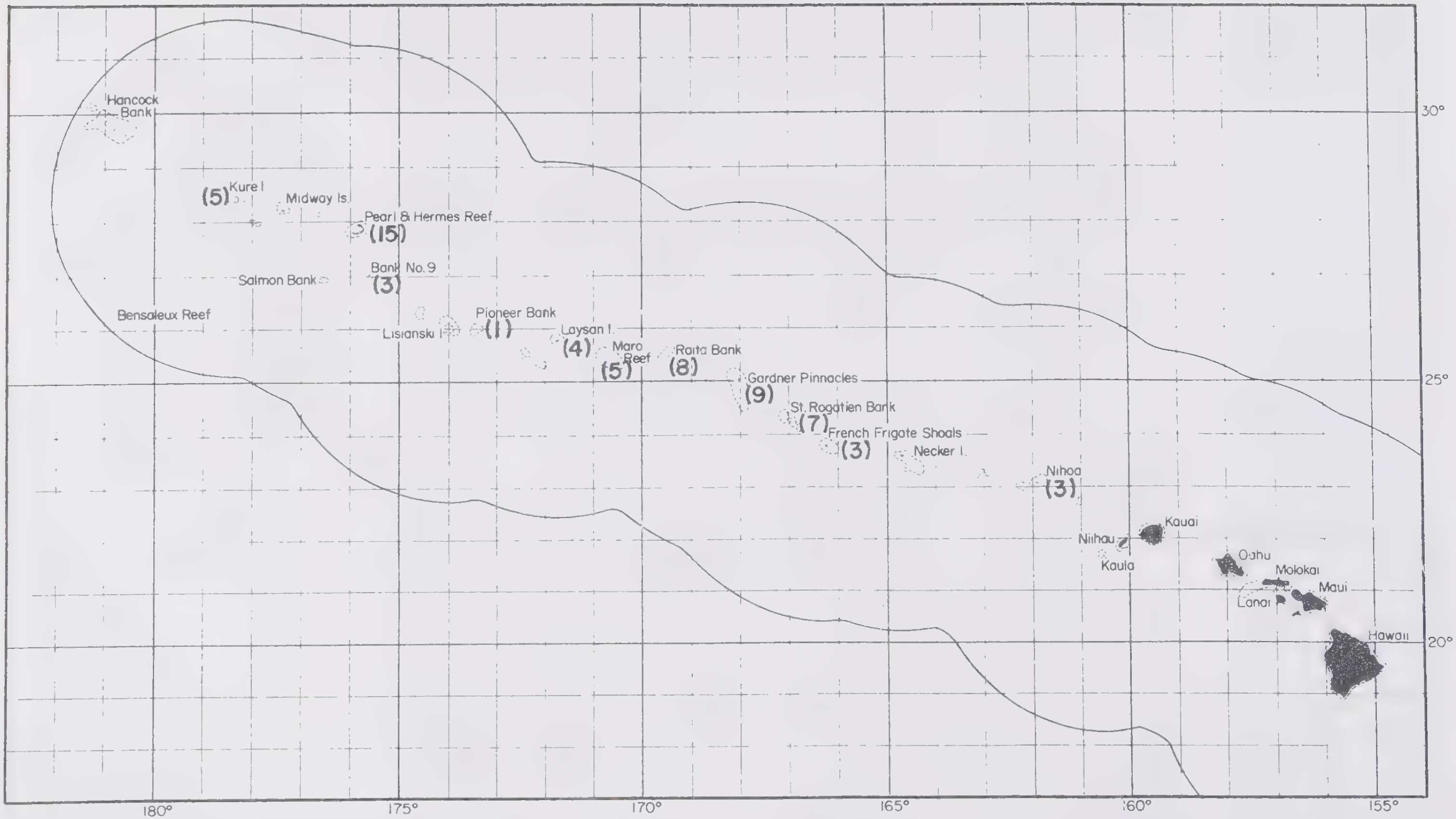
30°
25°
20°
180°
175°
170°
165°
160°
155°
Hancock Bank
(5) Kure I.
Midway Is.
Pearl & Hermes Reef
(15)
Salmon Bank
Bank No. 9
(3)
Bensaleux Reef
Pioneer Bank
(1)
Lisianski I.
Laysan I.
(4)
Maro Reef
(5)
Raita Bank
(8)
Gardner Pinnacles
(9)
St. Rogatien Bank
(7)
French Frigate Shoals
(3)
Necker I.
Nihoa
(3)
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Hawaii

Figure 1. The Northwestern Hawaiian Islands. The number of stomach samples collected at each bank is shown in parentheses.

length for all others. No attempt was made to measure the lengths of any prey items that were well digested.

Food items were identified to the lowest possible taxon using the methods of Harrison et al. (1983). When possible, fish were identified by external characteristics and morphometrics. In most cases, however, the fish were in an advanced stage of digestion and required clearing of the flesh and staining of the vertebrae with Alizarin S. A combination of vertebral counts and morphological characters was then used for identification. Invertebrates were identified by external morphological features; thus many of the crustaceans were identified at least to family since the exoskeletons remained intact or nearly intact despite digestion.

Many samples included bottom sediment and debris (classified as "rubble") which were saved for further identification of small infaunal invertebrates that may be of nutritional value to the predator. The volume of the rubble was determined by water displacement. The volume was also determined for unidentifiable digested remains.

DATA ANALYSIS

The importance of each of the forage items was determined by the method described by Pinkas et al. (1971), who developed the index of relative importance defined as

$$IRI = (N + V)F$$

where

N = Percentage of total aggregate number of a prey item

V = Percentage of total aggregate volume of a prey item

F = Percentage of occurrence of a prey item in the stomach samples

The IRI value provides a basis for ranking the prey items by incorporating the three measures traditionally used in stomach content analysis. Rubble and unidentified remains were not used in determining IRI.

RESULTS

The forage items found in the 64 stomach samples are listed in Table 1. The classification or taxonomic rank, the percent numerical, volumetric and frequency of occurrence, and the IRI values are given for each forage item.

TABLE 1. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME, AND INDEX OF RELATIVE IMPORTANCE VALUES OF THE FORAGE ITEMS IN 64 *PSEUDOCARANX DENTEX* FOOD SAMPLES

Forage Items	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
PHYLUM ANNELIDA							
Class Polychaeta	8	1.9	3	4.7	2.3	0.2	9.9
PHYLUM MOLLUSCA							
Class Gastropoda	18	4.3	10	15.6	1.2	0.1	68.6
Class Bivalvia							
Order Mytiloida							
Family Pinnidae							
Pinna muricata	2	0.5	2	3.1	14.0	1.4	5.9
Order Veneroida							
Family Cardiidae							
Nemocardium thaanumi	1	0.2	1	1.6	8.0	0.8	1.6
Class Cephalopoda	12	2.9	10	15.6	8.1	0.8	57.7
Order Octopoda	7	1.7	6	9.4	64.5	6.3	75.2
PHYLUM ARTHROPODA							
Class Crustacea	14	3.4	7	10.9	4.4	0.4	41.4
Subclass Malacostraca							
Order Amphipoda	1	0.2	1	1.6	0.1	<0.1	0.3
Order Stomatopoda	1	0.2	1	1.6	0.1	<0.1	0.3
Family Squillidae							
Lysiosquilla sp.	1	0.2	1	1.6	0.1	<0.1	0.3
Odontodactylus sp.	15	3.6	6	9.4	5.9	0.6	39.5
Pseudosquilla sp.	1	0.2	1	1.6	0.3	<0.1	0.3
Order Decapoda							
Suborder Natantia (shrimp)	14	3.4	5	7.8	3.5	0.3	28.9
Superfamily Caridea	15	3.6	3	4.7	6.0	0.6	19.7
Family Pandalidae	2	0.5	1	1.6	1.0	0.1	1.0
Family Crangonidae	2	0.5	1	1.6	0.4	<0.1	0.8
"Shrimp remains"	1	0.2	1	1.6	0.6	0.1	0.5
Suborder Reptantia							
Tribe Palinura							
Family Palinuridae							
Panulirus sp.	1	0.2	1	1.6	0.1	<0.1	0.3
Tribe Anomura							
Family Paguridae	2	0.5	2	3.1	1.6	0.2	2.2
Family Galatheidae							
Munida sp.	1	0.2	1	1.6	1.0	0.1	0.5
Tribe Brachyura	2	0.5	2	3.1	0.7	0.1	1.9
"Crab"	23	5.5	16	25.0	18.2	1.8	182.5
PHYLUM ECHINODERMATA							
Class Ophiuroidea	2	0.5	2	3.1	0.6	0.1	1.9
Class Echinoidea							
Order Cidaroida							
Family Cidaridae							
Prionocidaris hawaiiensis	1	0.2	1	1.6	5.5	0.5	1.1

TABLE 1. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME, AND INDEX OF RELATIVE IMPORTANCE VALUES OF THE FORAGE ITEMS IN 64 *PSEUDOCARANX DENTEX* FOOD SAMPLES (continued)

Forage Items	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
PHYLUM CHORDATA							
Superclass Pisces							
Class Osteichthyes							
(Unidentified fishes)	19	4.6	6	9.4	10.3	1.0	52.6
Order Anguilliformes	5	1.2	4	6.2	61.8	6.1	45.3
Family Congridae	30	7.2	5	7.8	55.7	5.5	99.1
Congrina aequoria	2	0.5	1	1.6	10.0	1.0	2.4
Family Ophichthidae	3	0.7	2	3.1	9.5	0.9	5.0
Muraenichthys cookei	2	0.5	1	1.6	7.0	0.7	1.9
"Leptocephalus larvae"	1	0.2	1	1.6	0.8	0.1	0.5
Order Myctophiformes							
Family Synodontidae	5	1.2	2	3.1	60.1	5.9	21.3
Family Chlorophthalmidae	1	0.2	1	1.6	2.5	0.2	0.6
Family Myctophidae	1	0.2	1	1.6	0.5	<0.1	0.3
Order Gadiformes							
Family Moridae	1	0.2	1	1.6	37.0	3.6	6.1
Family Ophidiidae	27	6.5	3	4.7	7.9	0.8	34.3
Order Lophiiformes							
Family Ogcocephalidae	2	0.5	1	1.6	1.6	0.2	1.1
Halieutaea retifera	1	0.2	1	1.6	3.5	0.3	0.8
Malthopsis sp.	1	0.2	1	1.6	0.3	<0.1	0.3
Order Scorpaeniformes							
Family Scorpaenidae	7	1.7	2	3.1	26.6	2.6	13.3
Order Dactylopteriformes							
Family Dactylopteridae							
Dactyloptena orientalis	1	0.2	1	1.6	1.3	0.1	0.5
Order Pegasiformes							
Family Pegasidae							
Pegasus papilio	2	0.5	2	3.1	0.8	0.1	1.9
Order Perciformes							
Family Serranidae	13	3.1	4	6.2	8.6	0.8	24.2
Anthias sp.	3	0.7	3	4.7	6.4	0.6	6.1
Family Priacanthidae							
Priacanthus sp.	12	2.9	1	1.6	207.0	20.4	37.3
Family Lutjanidae	16	3.9	3	4.7	9.1	0.9	22.6
Symphysanodon sp.	5	1.2	1	1.6	7.7	0.8	3.2
Family Percophididae (= Bembropsidae)	1	0.2	1	1.6	2.3	0.2	0.6
Family Ammodytidae							
Embolichthys sp.	12	2.9	3	4.7	53.9	5.3	38.5
Order Gobiesociformes							
Family Callionymidae	1	0.2	1	1.6	0.8	0.1	0.5
Order Pleuronectiformes							
Family Bothidae	7	1.7	6	9.4	20.8	2.0	34.8
Bothus thompsoni	1	0.2	1	1.6	1.0	0.1	0.5
Order Tetraodontiformes							
Family Monacanthidae	2	0.5	1	1.6	8.0	0.8	2.1
Family Tetraodontidae	18	4.4	5	7.8	18.1	1.8	48.4
Fish remains	—	—	6	9.4	5.3	0.5	—
"Rubble"	—	—	20	31.2	21.9	2.2	—
Unidentified remains	—	—	43	67.2	194.1	19.1	—

Table 2 presents the analysis of food items by major classes and the ranks of the forage items in descending order of IRI values for the invertebrates and fishes. Fish prey were primarily grouped at the family level and the invertebrates primarily at the class or order level.

Fishes, molluscs, and crustaceans formed the bulk of the forage items in the samples. Fish prey yielded a total IRI value of 7,884.5 compared with 1,454.9 for crustaceans and 653.6 for molluscs.

Fishes as a whole occurred in 68.8 percent of the stomach samples and represented 64.2 percent of the total aggregate volume, and 50.4 percent of the total number of forage items. Twenty families of fishes were represented, and families that had high IRI values were Congridae (IRI = 133.5), Priacanthidae (IRI = 74.7), and Serranidae (IRI = 58.9). Unidentified fish (IRI = 52.6) which were also included in the analysis deserve mention only to the extent that individuals which comprised this group were not of the same species, but of various species.

The invertebrate forage included four phyla, with the majority belonging to Arthropoda, class Crustacea. Crustaceans appeared in 53.1 percent of the samples and represented 4.3 percent of the total aggregate volume and 23.1 percent of the total forage items. Among the crustaceans, crabs (suborder Reptantia) ranked the highest (IRI = 277.7), followed by shrimp (suborder Natantia) (IRI = 131.1), of which most were carideans. Stomatopods (primarily _Odontodactylus_ sp.) and an amphipod were also found.

Molluscs were present in 34.4 percent of the samples and comprised 9.4 percent of the total volume and 9.6 percent of the total number of forage organisms. Cephalopods (IRI = 256.2), mainly octopods (IRI = 75.2), were the primary contributor from this phylum appearing in 21.9 percent of the samples and representing 7.1 percent of the total aggregate volume. Gastropods and bivalves were also present.

Other invertebrates were minor contributors to the diet of the white trevally sampled. These included eight polychaetes (IRI = 9.9) and three echinoderms (IRI = 6.1); together they comprised 2.6 percent of the forage items, 0.8 percent of the total aggregate volume, and appeared in 9.4 percent of the samples. Many small invertebrates and limestone fragments were found in the rubble. A list of these organisms (identified through the courtesy of B. Burch, Bishop Museum, Honolulu, Hawaii) and their taxonomic rank are presented in Appendix 1.

To examine differences in diet with respect to location of capture, the islands and banks were divided into three geographical regions as described by Moffitt (1980) (Table 3). Region 1 ranges from Nihoa to Gardner Pinnacles and represents the area in the NWHI fished most by commercial vessels in recent years,

TABLE 2. NUMBER, FREQUENCY OF OCCURRENCE, VOLUME, AND INDEX OF RELATIVE IMPORTANCE VALUES OF MAJOR CLASSES OF FORAGE ITEMS IN 64 *PSEUDOCARANX DENTEX* FOOD SAMPLES

Forage Classes	No. of Organisms		Occurrence		Aggregate Total Volume		IRI
	Total	Percent	No.	Percent	ml	Percent	
INVERTEBRATES							
Reptantia "crabs"	28	6.8	20	31.2	21.5	2.1	277.7
Cephalopoda	19	4.6	14	21.9	72.6	7.1	256.2
Natantia (shrimp)	34	8.2	9	14.1	11.5	1.1	131.1
Stomatopoda	18	4.3	9	14.1	6.4	0.6	69.1
Gastropoda	18	4.3	10	15.6	1.2	0.1	68.6
Crustacea (unidentified)	14	3.4	7	10.9	4.4	0.4	41.4
Bivalvia	3	0.7	3	4.8	22.0	2.2	13.9
Annelida (Polychaeta)	8	1.9	3	4.7	2.3	0.2	9.9
Echinodermata	3	0.7	3	4.7	6.1	0.6	6.1
Amphipoda	1	0.2	1	1.6	0.1	<0.1	0.3
Reptantia "lobsters"	1	0.2	1	1.6	0.1	<0.1	0.3
FISHES							
Congridae	32	7.7	6	9.4	65.7	6.5	133.5
Priacanthidae	13	3.1	2	3.1	213.6	21.0	74.7
Serranidae	16	3.9	7	10.9	15.0	1.5	58.9
Osteichthyes (Unidentified fishes)	19	4.6	6	9.4	10.3	1.0	52.6
Tetraodontidae	18	4.3	5	7.8	18.1	1.8	47.6
Anguilliformes (Unidentified eels)	5	1.2	4	6.2	61.8	6.1	45.3
Bothidae	8	1.9	7	10.9	21.8	2.1	43.6
Lutjanidae	21	5.1	4	6.2	16.8	1.6	41.5
Ammodytidae	12	2.9	3	4.7	53.9	5.3	38.5
Ophidiidae	27	6.5	3	4.7	7.9	0.8	34.3
Synodontidae	5	1.2	2	3.1	60.1	5.9	22.0
Scorpaenidae	7	1.7	2	3.1	26.6	2.6	13.3
Ophichthidae	5	1.2	2	3.1	16.5	1.6	8.7
Moridae	1	0.2	1	1.6	37.0	3.6	6.1
Ogcocephalidae	4	1.0	2	3.1	5.4	0.5	4.6
Monacanthidae	2	0.5	1	1.6	8.0	0.8	2.1
Pegasidae	2	0.5	2	3.1	0.8	0.1	1.9
Chlorophthalmidae	1	0.2	1	1.6	2.5	0.2	0.6
Percophididae (= Bembropsidae)	1	0.2	1	1.6	2.3	0.2	0.6
Dactylopteridae	1	0.2	1	1.6	1.3	0.1	0.5
Leptocephalus larvae	1	0.2	1	1.6	0.8	0.1	0.5
Callionymidae	1	0.2	1	1.6	0.8	0.1	0.5
Myctophidae	1	0.2	1	1.6	0.5	<0.1	0.3
Fish remains	—	—	6	9.4	5.3	0.5	—
OTHERS							
"Rubble"	—	—	20	31.2	21.9	2.2	—
Unidentified remains	—	—	43	67.2	194.1	19.1	—

TABLE 3. RANKS AND INDEX OF RELATIVE IMPORTANCE VALUES OF THE MAJOR FORAGE CLASSES OF PREY ITEMS BY REGION

Forage Classes	Region 1 (n = 22)		Region 2 (n = 18)		Region 3 (n = 23)	
	Rank	IRI	Rank	IRI	Rank	IRI
INVERTEBRATES						
Annelida (Polychaeta)	12	1.6	11	2.6	—	—
Gastropoda	9	4.6	9	4.7	5*	15.5
Bivalvia	7	5.8	—	—	15	1.6
Cephalopoda	—	—	5*	14.4	6	15.0
Octopoda	2*	58.6	—	—	—	—
Crustacea (unidentified)	17	0.4	12	2.4	4*	17.2
Amphipoda	—	—	21	0.4	—	—
Stomatopoda	17	0.4	20	0.4	2*	48.5
Natantia (shrimp)	1*	77.7	—	—	11	4.9
Reptantia "lobsters"	—	—	—	—	22	0.4
Reptantia "crabs"	3*	37.6	7	7.4	1*	59.3
Echinodermata	11	3.2	—	—	21	0.4
FISHES						
Osteichthyes (Unidentified fishes)	6	6.2	13	1.9	9	9.5
Anguilliformes (Unidentified eels)	—	—	21	0.4	12	2.9
Congridae	—	—	1*	132.9	—	—
Ophichthidae	10	3.4	18	1.0	—	—
"Leptocephalus larvae"	—	—	—	—	20	0.5
Synodontidae	—	—	19	0.9	8	10.2
Chlorophthalmidae	—	—	—	—	17	0.8
Myctophidae	16	0.4	—	—	—	—
Moridae	—	—	8	6.0	—	—
Ophidiidae	—	—	10	4.3	7	14.2
Ogcocephalidae	—	—	17	1.0	16	1.3
Scorpaenidae	5*	13.5	—	—	—	—
Dactylopteridae	—	—	—	—	19	0.6
Pegasidae	—	—	15	1.8	—	—
Serranidae	8	5.7	16	1.1	3*	17.5
Priacanthidae	13	1.4	2*	36.2	—	—
Lutjanidae	4*	25.9	14	1.9	—	—
Percophididae	15	0.7	—	—	—	—
Ammodytidae	—	—	3*	24.4	18	0.6
Callionymidae	—	—	—	—	20	0.5
Bothidae	—	—	6	13.3	10	9.0
Monacanthidae	—	—	—	—	13	2.0
Tetraodontidae	14	1.1	4*	15.1	14	1.8

*Highest ranked classes for each region

Region 2 is from Raita Bank to Lisianski Island, and Region 3 is from Pearl and Hermes Reef to Kure Atoll. The latter two regions are separated by a natural break in the chain. The IRI values of the prey classes for each region were used to rank the importance of the classes in the three regions. The highest value was given the rank of 1. The top ranked classes in Regions 1 and 3 were invertebrates, primarily crustaceans. The top classes in Region 2 were fishes (Congridae, Priacanthidae, Ammodytidae, and Tetraodontidae).

The lengths of fish prey ranged from 14 mm (*Pegasus papilio*) to 306 mm (an ophichthid eel). Lengths of invertebrate forage items ranged from 5 mm (a crangon shrimp) to 42 mm (a stomatopod, *Odontodactylus* sp.). Measurements, ranges, and mean lengths of prey items are presented in Table 4.

DISCUSSION

The results of this diet study indicate that as in other carangids previously studied, the white trevally is a high-level opportunistic carnivore. The species is primarily piscivorous, although cephalopods and crustaceans are also major contributors to their diet. The results also strongly indicate that this species is a bottom feeder. By comparison, Randall (1967) noted small amounts of sand in a few stomachs of *Caranx ruber*, indicating that at times they were feeding on prey directly off the bottom. The presence of some coral tissue and algae provided evidence that *C. ignobilis* also forage occasionally on the bottom (Williams, 1965). In this study, the presence of rubble in about 31 percent of the samples shows that the white trevally feeds on the bottom to an even greater degree.

Nineteen of the 20 fish families found in the forage can be classified as benthic, the exception being myctophids, which although inhabiting the water column, may approach the bank slopes during their vertical migrations. Nearly half of the fish families represented in the diet of white trevally were also represented in the food of another bottom feeder, *E. quernus* (see paper on grouper in this proceedings by Seki). Fishes of the Congridae and Serranidae families, which were two of the most important groups in the diet of the white trevally, were also among the most important fishes in the *E. quernus* stomach samples.

The bottom feeding behavior of white trevally is also reflected in the invertebrate forage. The invertebrates with the highest IRI ranking were crabs, octopi, and gastropods, all bottom dwellers. The occurrence of other invertebrates such as echinoderms, bivalves, and shrimp (even if taken infrequently) in the forage composition reflects the probable browsing behavior of the species. It is noteworthy that among the outstanding morphological features of white trevally are the thick, fleshy lips on a mouth that features an inferior jaw, uncharacteristic of most other carangids. This morphology would appear to facilitate bottom browsing.

the number of stomach samples was inadequate to demonstrate possible selective feeding or other trends.

A small sample size also prohibited an investigation of the extent stomach contents are influenced by seasonal effects. Although sampling was conducted throughout the year, 37 (58 percent) of the stomachs were collected in the summer. For the other seasons, 15 (23 percent) were collected in the spring, 9 (14 percent) in the fall, and 3 (5 percent) in the winter.

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APPENDIX A.

Components of rubble found in *Pseudocaranx dentex* stomachs. (Identified through the courtesy of B. Burch, Bishop Museum, Honolulu, Hawaii)

- Limestone "rubble"
- Phylum Protozoa
  - Order Foraminifera
    - Family Nummulitidae
      - *Heterostegina depressa*
    - Family Homotrematidae
      - *Miniacina miniacea*
    - Family Amphisteginidae
      - *Amphistigina* cf. *bicirculata*
    - Family Soritidae
      - *Marginopora vertebralis*

- Phylum Coelenterata
  - Order Scleractinia
    - Family Fungiidae (coral)
      - *Cycloseris fragilis*

- Phylum Echinodermata
  - Class Echinoidea
    - Family Cidaroidae
    - Family Fibulariidae
      - *Echinocyamus elongatus*
  - Class Ophiuroidea

- Phylum Mollusca
  - Class Gastropoda
    - Family Strombidae
      - *Strombus helli*
    - Family Eulimidae
    - Family Atyidae
    - Family Naticidae (Natica)
    - Family Cerithiidae
    - Family Littorinidae
      - ?*Peasiella tantilla*
    - Family Epitoniidae
    - Family Hipponicidae
      - *Sabia conica*
    - Family Xenophoridae
      - *Xenophora peroniana*
    - Family Triphoridae
      - *Triphora* cf. *tubularis*
    - Family Columbellidae
    - Family Pteropoda
    - Family Bursidae
      - *Gyrineum pusillum*
    - Family Turbinidae
      - *Gibbula marmorea*
    - Family Rissoidae
      - *Zebina tridentata*
    - Family Turridae
  - Class Bivalvia
    - Family Ostreidacea
    - Family Cardiidae
      - *Nematocardium thaanumi*
    - Family Spondylidae
      - *Spondylus linguafelis*
    - Family Carditidae
      - *Carditella* sp.
    - Family Mytilidae
      - *Brachidontes crebrestriatus*
    - Family Arcidae
    - Family Pectinidae
    - Family Pinnidae
  - Class Scaphopoda
    - Family Dentalidae

- Phylum Arthropoda
  - Class Crustacea
  - Order Amphipoda
    - Family Gammaridae
  - Tribe Brachyura
    - Family Xanthidae
    - Family Portunidae
    - Family Leucosiidae
  - Tribe Anomura
    - Family Paguridea

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[PANEL DISCUSSION.] Optimum use scenarios

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INTRODUCTION

The charge to the members of this panel is for each to provide a personal view of how the resources of the Northwestern Hawaiian Islands (NWHI) can be best utilized. It should be emphasized that the viewpoints expressed in my presentation are strictly my own and do not represent those of the National Marine Fisheries Service (NMFS).

I am pleased that the discussion is organized around the concept of an optimal use strategy rather than that of advocacy positions. The former provides a more positive outlook, whereas the latter suggests a process of tearing down the opposition to make a point.

It is difficult to develop an acceptable optimal use scenario since there are many and varied interest groups to consider, and the scenario should consider the merits of consumptive and nonconsumptive resources. The interest groups include the military, commercial and recreational fishing interests, conservationists, preservationists, and the public-at-large. On the one hand the commercial interests would argue that the resources should be made accessible to provide food. They would make a further point that developing a fishery in the Northwestern Hawaiian Islands will expand Hawaii's economic base and reduce the state's reliance on imported fishery products. On the other hand, conservationists are concerned about the nonconsumptive resources and would like to see these resources maintained at optimum population levels. Of special concern are the Hawaiian monk seal and green sea turtle. Discounting the extremists, most people would like to see both objectives achieved, that is, to utilize as much of the fishery resources of the region without adversely affecting the nonconsumptive resources.

PROPOSED SCENARIO

The optimal use scenario I propose is (1) to develop Midway Islands as a major U.S. fishing base in the central North Pacific; (2) to refrain from developing all the other emerged lands of the Northwestern Hawaiian Islands, that is, allow no fishing bases or human habitation; (3) to encourage the utilization of the deep-water fishery resources, including the snappers, groupers, tunas, lobsters, and shrimp; and (4) to approach the utilization of the nearshore resources cautiously. Caution is needed to evaluate nonconsumptive resources, e.g., seabirds, Hawaiian monk seals, and green sea turtles.

The optimal use scenario I propose is based upon an assessment of the present fish marketing structure, a projection of what might happen if a number of assumptions I make are correct, and finally on a review of fishery development in the context of the nature and size of the resources in the Northwestern Hawaiian Islands.

At present, there is a limited market in Hawaii for fresh fish, especially the higher-priced snappers and groupers. If one were to discount the restaurant trade, I would guess that the consumers of fresh fish would form a pocket market. By this I mean that the demand for fresh bottomfish is not widespread. Although one could presumably overcome the marketing problem by education and promotion, a more critical problem is that of the relatively short shelf life of these species. Shelf life is of economic concern to the producers, that is, the fishermen, the dealer, and the consumer. It has been reported that the shelf life of bottomfish is about 12 days. When one considers the relatively great distance between the Northwestern Hawaiian Islands and the population centers in the state, and that the population in Hawaii is scattered over several islands, the short shelf life represents a critical problem in developing the fishery.

Within the size limits of the fishery resources in the NWHI, the growth of the fishery, in my opinion, will be dependent upon the expansion of the frozen-fish market. The expansion certainly will be dependent upon whether fish from the NWHI can be harvested and sold as frozen products at prices that are competitive with those of imported frozen-fish products. I should note that considerable advances have been made in recent years in handling and freezing fish. For example, if one agrees that the Japanese are connoisseurs of fresh fish, and a hundred million Japanese can't be wrong, then the fact that the bulk of the fish that is consumed as sashimi in Japan is landed as frozen tuna clearly demonstrates the potential for freezing fish in Hawaii.

If my premise is correct that at present there is a limited market for fresh fish in Hawaii and that the future expansion of the fishing industry to the Northwestern Hawaiian Islands depends on the development of a market for frozen fish, then the need for fishing bases in the NWHI takes on a new perspective.

Weather considerations and the lack of safe anchorages in the Northwestern Hawaiian Islands will generally restrict fishing in the area to larger vessels. Although I have not worked out the economics, I would guess that a vessel which would be capable of bottomfishing in the NWHI would probably be equipped with freezing facilities. Rather than having the catch trans-shipped from a fishing base in the NWHI, it would more likely land the catch at a port in the main islands.

Given my comments on why I do not envision a fishing base in the lower reaches of the Northwestern Hawaiian Islands, I would now like to review the resources and indicate why I feel that a fishing base at Midway Islands would be advantageous in the development of fisheries for tunas, squids, seamount resources, precious coral, spiny lobster, shrimp, deep-water fishes, and nearshore fishes.

TUNAS

For tunas we have an albacore fishery located north of the Hawaiian Archipelago at about 30°N latitude and higher. The albacore is a highly prized species with an estimated fishable stock of about 100,000 tons in the North Pacific. The U.S. catch in recent years has been in the neighborhood of 10,000 to 20,000 tons. Of this U.S. total, approximately 2,000 tons has been taken in recent years from the area north of Midway Islands. The U.S. boats in the fishery are small troll or jig boats with carrying capacities of about 30 to 60 tons. The catch is frozen on board the ship. Because of its limited capacity these albacore boats generally have to return to port several times during the fishing seasons to discharge their catch, refuel, and resupply.

In 1979, Castle and Cooke provided a mothership which operated out of Midway Islands. With a mothership, the albacore boats were able to discharge their catch at Midway Islands and obtain fuel and supplies without traversing great distances. During other years the boats had to go to Dutch Harbor (Alaska) or to Honolulu to land the catch, refuel, and resupply. Thus one can see the advantages of having a base at Midway Islands.

Based on Japanese pole-and-line fishing records, the center of skipjack tuna abundance appears to be around latitude 20°N. Skipjack tuna are also caught in the immediate vicinity of the Northwestern Hawaiian Islands. In considering the development of a Hawaii-based pole-and-line fishery to harvest this species, baitfish is a major problem. I will not go into further details of the skipjack tuna resource or discuss the yellowfin tuna resource, other than to note that purse seining is becoming the principal method of fishing for both in the central and western Pacific. It has been suggested that small purse seiners probably could operate economically in the NWHI. Thus, the albacore fishery and to a limited extent a small vessel purse seine fishery for skipjack and yellowfin tunas could make use of a base at Midway Islands.

SQUID

In recent years, fishermen from Japan as well as Taiwan have developed a fishery for squid in the higher latitudes of the central North Pacific. The squid are taken with jigging machines or gill nets. My only comment here is that a potential for a U.S. squid fishery exists in the area north of the Northwestern Hawaiian Islands. Midway Islands could serve a squid fishery in the same way it would the tuna fisheries.

SEAMOUNT RESOURCES

The seamount resources are principally armorhead and alfonsin which are taken on a number of seamounts in the central North Pacific. In recent years the Japanese have been trawling for armorhead and alfonsin in the Hancock Seamounts area. The annual catch has been less than the U.S. allocation of 1,000 tons. Similar to the squid fishery, there is a potential for the development of a U.S. fishery for armorhead and alfonsin. A base at Midway Islands would prove invaluable, especially if smaller vessels are utilized.

PRECIOUS CORAL

Several years ago foreign fishermen fishing illegally within the Hancock Seamounts area discovered new beds of precious coral in deep waters (1,000 to 1,500 m). Information on the extent of this resource is not available. Again, the precious coral represents another fishery that could be developed by U.S. interests using small fishing vessels.

SPINY LOBSTERS

At present, the spiny lobsters from the Northwestern Hawaiian Islands are being marketed live and as frozen tails. Should the market for live lobsters increase greatly, a fishing base at Tern Island could be valuable. However, if development of the frozen tail market is greater, then the need for a base at Tern Island or Midway Islands would be minimal.

SHRIMPS

Considering the very short shelf life of fresh shrimp, development of a fishery in the Northwestern Hawaiian Islands would be based on the marketing of a frozen product. A shrimp fishery, if it develops, would be capable of operating independently from a base at Tern Island or Midway Islands.

DEEP-WATER FISHES

My views of the market for the deeper-water snappers and groupers have already been presented.

NEARSHORE FISH RESOURCES

While the species composition of the nearshore fauna is different from that of the deeper-water fauna, many of the problems noted in marketing and developing the deep-water fishery resources in the Northwestern Hawaiian Islands would also prevail for the nearshore resources. One further consideration is that the effect on the nonconsumptive resources in the NWHI is much greater for the nearshore resources than it is for the deeper-water fishes. This would need to be taken into consideration in any decision on the development of fishing bases.

NONCONSUMPTIVE RESOURCES

I would like to conclude my discussion on resoures with a brief review of the nonconsumptive resources. My guess is that there are very few commercial or recreational fishermen who would take the extreme position of not caring at all about the fate of nonconsumptive resources. In fact, most commercial pole-and-line tuna fishermen are very concerned about the well being of seabirds since they depend on the flocks of feeding seabirds to locate tuna schools. For those whose priorities lean towards the nonconsumptive resources, the best thing that could happen perhaps is that no fishing bases at all would be established in the Northwestern Hawaiian Islands.

The major concern in establishing a fishing base at Tern Island would primarily be its effect on the green turtle and monk seal populations at French Frigate Shoals. The Honolulu Laboratory of NMFS is currently undertaking a study to assess the stock size of the green sea turtle. Unfortunately, French Frigate Shoals, which has been identified as the major nesting site for the green turtle, is being considered as a site for a fishing base. If one were to guess the adult turtle population in the Northwestern Hawaiian Islands I would venture to say that the figure was around 1,500 animals. Thus, for the turtles, it appears that French Frigate Shoals is extremely important. For the Hawaiian monk seal a similar situation exists in that French Frigate Shoals supports the largest fraction of the monk seal population in the chain. Based on recent animal counts, the French Frigate Shoals population represents more than 53 percent of the total population.

The question may be raised as to what effect the development of a fishing base at Midway Islands would have on the nonconsumptive resources of the region. As most of you are aware, Midway Islands has been and still is a military base; thus, people have lived there for a long time. Whether this has resulted in the present low number of turtles and monk seals is not a point that I wish to argue. It should only be noted that currently turtles and monk seals are not numerous at Midway Islands. For seabirds, the most abundant species are the Laysan and black-footed albatrosses. Roughly 40 percent of the total albatrosses counted in the Northwestern Hawaiian Islands are on Midway Islands. From all accounts the albatross population appears to be holding its own despite the presence of humans at Midway Islands. Other species that make up a large percentage of the seabird population in the NWHI include the red-tailed tropic bird, sooty tern, and white terns.

CONCLUSION

In summary, I hope I have made a case for the establishment of a single fishing base in the Northwestern Hawaiian Islands. A fishing base at Midway Islands would meet the needs of fishery development in the region while minimizing the impact on the non-consumptive resources in the area. Given the projected future direction that the fishing industry will probably be taking, there appears to be no need for a fishing base in other sectors of the Northwestern Hawaiian Islands.

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Estimating the Dolphin Population Size Yielding Maximum Net Production

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ABSTRACT

A method is presented for estimating maximum net productivity level by comparing gross reproductive rates in three populations at different proportions of original size.

INTRODUCTION

The population size at which the absolute rate of change of population size is largest (maximum net productivity level or MNPL) is interesting both theoretically and in applied population assessments (Holt and Talbot, 1978; Smith and Fowler, 1981). Some general hypotheses have been developed about the relationship of MNPL and equilibrium population sizes (e.g. Gilpin and Ayala, 1976; Fowler, 1981). Fowler tested the hypotheses that density-dependent changes in vital rates, and hence MNPL, occur at a large fraction of equilibrium population size for long-lived species. He concluded that MNPL occurs at population sizes greater than one half, and likely quite near, equilibrium population size.

Few direct estimates of MNPL are available for long-lived species, and virtually none are available for cetaceans. In this paper I describe a method of estimating MNPL for dolphins in the eastern tropical Pacific Ocean, using data on the history of exploitation and the observed vital rates of different but related populations. An example is given using gross reproductive rates for three populations of spinner dolphin (*Stenella longirostris*).

MATERIALS AND METHODS

Dolphins of several species have been killed incidentally to tuna fishing in the eastern tropical Pacific tuna purse seine fishery since the late 1950s. The status of three populations of the spinner dolphin, *S. longirostris*, is described in Smith (1979; 1983). These three populations have been subjected to this incidental mortality for different lengths of time; one population, the eastern spinner dolphin, has been involved since 1959, while two other populations, the northern and southern whitebelly spinner dolphins, have been involved since approximately 1969 and 1973, respectively.

Estimates of the numbers of spinner dolphins killed in this fishery have been made as the product of the mean number of dolphins killed per net set observed aboard fishing vessels and the numbers of net sets made each year. Estimates from Smith (1979) are shown in Fig. 1 for each population. The numbers killed were very high in the 1960s and decreased markedly in the 1970s.

Estimates of the sizes of the three populations in 1979 (Table 1) were made from aerial and research-vessel dolphin-sighting survey data (Holt and Powers, 1982). Estimates of the gross reproductive rates (Table 1) of these three populations were made from data from samples of dolphins killed in the fishery (Perrin, Holts and Miller, 1977; Smith, 1979). The more heavily exploited eastern and whitebelly spinner dolphin populations have higher estimated reproductive rates. However, alternate methods of estimating these rates yield different results, and there is considerable uncertainty as to the appropriate estimates (Smith, 1979; Perrin and Reilly, 1984). The values used were selected to illustrate the method of estimating MNPL being described.

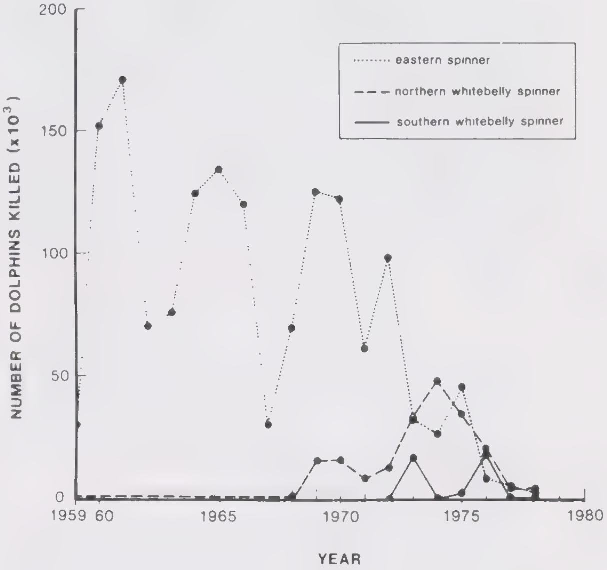

Fig. 1. Estimated numbers of spinner dolphins (*Stenella longirostris*) killed from three populations, from 1959 to 1978, incidental to yellowfin tuna purse seine fishing in the eastern tropical Pacific, from Smith (1979).

Table 1

Estimates of population size in 1979, from Holt and Powers (1982), and average reproductive rate from 1973–1978, from Smith (1979), for three populations of spinner dolphin (*Stenella longirostris*) in the eastern tropical Pacific

Spinner population	Population size (× 1,000)	Gross reproductive rate
Eastern	305	0.098
Northern whitebelly	401	0.088
Southern whitebelly	223	0.067

The estimates of dolphins killed (Fig. 1), 1979 population size (Table 1), and gross reproductive rates

(Table 1) can be used to estimate successive population sizes as

$$N_{t+1} = N_t + (\gamma - \mu) N_t - K_t = N_t(1+\rho) - K_t, \quad (1)$$

where N = population size, in numbers; t = year; γ = gross reproductive rate; μ = natural mortality rate; K = number of dolphins killed by fishery; $\rho = \gamma - \mu$ = net recruitment rate.

In this model recruitment and natural mortality occur simultaneously, with rates applying to the whole population, not just the reproductive portion, at the beginning of the time interval. The catch is assumed to be taken after recruitment and natural mortality have occurred. This model applies only approximately to the incidental killing of dolphins in the eastern tropical Pacific in that recruitment and the incidental mortality occur simultaneously; similarly, the model does not account for age-structure changes which might affect the proportion mature. However, for this example these simplifying assumptions will suffice (Smith and Polacheck, 1979).

Solving equation 1 for the population size in previous years,

$$\hat{N}_t = \frac{N_0}{\prod_{i=1}^{t} (1+\rho_i)} + \sum_{j=1}^{t} \frac{K_j}{\prod_{i=1}^{j} (1+\rho_i)}, \quad (2)$$

where N_0 is the population size in 1979, N_t denotes the to-be-estimated population size, t years earlier, and ρ_i denotes the net recruitment rate in the ith year prior to 1979. The properties of this estimate are explored in Smith and Polacheck (1979).

Values of the reproductive rate for each year can be obtained by assuming that the gross reproductive rate is a function of population size,

$$\rho(N) = \gamma(N) - \mu, \quad (3)$$

where $\rho(N)$ = net recruitment rate as a function of population size N, $\gamma(N)$ = gross reproductive rate.

A suitable model for $\gamma(N)$ is given by Allen (1976),

$$\gamma(N) = (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N}{\phi}\right)^{\zeta}\right) + \gamma_1, \quad (4)$$

where γ_0 = gross reproductive rate for N near zero; γ_1 = gross reproductive rate at equilibrium population size ϕ, ζ = shape parameter for changes in gross reproductive rate.

The shape of this relationship is shown in Fig. 2 for several values of the shape parameter ζ.

An expression for the net recruitment rate as a function of population size is obtained by substituting $\gamma(N)$ from equation 4 into equation 3,

$$\rho(N) = (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N}{\phi}\right)^{\zeta}\right) + \gamma_1 - \mu \quad (5)$$

The net recruitment rate must be zero when $N = \phi$, implying that $\gamma_1 = \mu$. That is, the gross reproductive rate at the equilibrium population size is the same as the natural mortality rate.

An expression for historical population sizes as a function of several estimated parameters and four unknown parameters is obtained by substituting $\rho(N)$ from equation 5, noting $\gamma_1 = \mu$, into equation 2. The unknown parameters are γ_0, γ_1, ζ and ϕ.

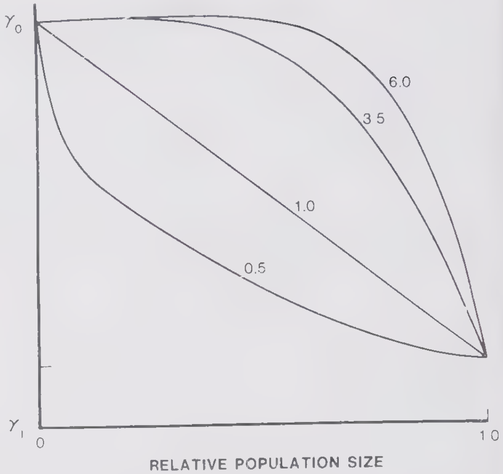

Fig. 2. The gross reproduction rate γ in equation 4 as a function of population size, relative to equilibrium population size (N/ϕ), for values of the shape parameter ζ = 0.5, 1.0, 3.5, and 6.0.

$$\hat{N}_t(\gamma_0, \gamma_1, \zeta, \phi) = \frac{N_0}{\prod_{i=1}^{t}\left(1 + (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N_i}{\phi}\right)^{\zeta}\right)\right)} + \sum_{j=1}^{t} \frac{K_j}{\prod_{i=1}^{j}\left(1 + (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N_i}{\phi}\right)^{\zeta}\right)\right)} \quad (6)$$

The equilibrium population size ϕ in equation 6 can be estimated from equation 6 itself, by taking t to be the year exploitation began for each population. That is,

$$\hat{\phi} = N_t(\gamma_0, \gamma_1, \zeta, \hat{\phi}), \quad (7)$$

where t is sufficiently large, for given values of γ_0, γ_1, and ζ. This equation must be solved iteratively.

Values for the remaining three unknown parameters in equation 6, γ_0, γ_1, and ζ, can be obtained by minimizing the differences between estimates of gross reproductive rates for the three populations (Table 1) and the modeled values of gross reproductive rate from equation 4. For convenience, the sum of squares of differences can be minimized,

$$\sum_{i=1}^{3} \left(\hat{G}_i - (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N_{0i}}{\hat{\phi}_i}\right)^{\zeta}\right)\right)^2, \quad (8)$$

where i (= 1, 2, 3) denotes the population, G_i denotes the observed gross reproductive rate for the ith population, and $\hat{\phi}_i$ is obtained from equation 7 for each of the three populations.

Minimization of equation 8 involves evaluating the sum of squares for all possible values of γ_0, γ_1 and ζ. For each population for each set of values of γ_0, γ_1 and ζ, equation (7) must be solved, iteratively as noted above. Due to the complexity of the equations and the illustrative nature of the calculations, the values of γ_0, γ_1 and ζ yielding a minimum value for equation (8) were determined by direct examination of the sum of squares surface. Thus the solution obtained is not exact, and no variances have been calculated.

The value of ζ which minimizes equation 8 implies a value of MNPL. This value can be determined by substituting $\rho(N)$ from equation 5 into equation 1, and solving for the population size with maximum rate of change (Allen, 1976), yielding

$$\psi = \phi\left(\frac{1}{\zeta+1}\right)^{\frac{1}{\zeta}}, \tag{9}$$

where ψ denote the maximum net productivity level (MNPL) in numbers of animals.

RESULTS

Using estimates of the number of dolphins killed incidentally (K_j, Fig. 1), the 1979 population sizes (Table 1) and the gross reproduction rates (G_i, Table 1), the estimated values of the gross reproductive rates at population sizes near zero and near equilibrium (γ_0 and γ_1, respectively) and the estimate of the shape parameter (ζ) are obtained from equations 6, 7 and 8 (Table 2). The fit of equation 4 to the observed estimates of gross reproductive rate is shown in Fig. 3. Although the deviations about the line are too small to be apparent in the graph, there is some lack of fit. The maximum net productivity level corresponding to $\zeta = 8.0$, as a fraction of the equilibrium population size, ψ/ϕ, given in Table 2, is obtained from equation 9.

The estimated equilibrium population sizes, $\hat{\phi}$ in equation 6, corresponding to the parameter estimates in Table 2, are 1,330, 490, and 240 thousand dolphins, for eastern spinner, northern whitebelly spinner, and southern whitebelly spinner dolphins, respectively (Table 3). The corresponding maximum net production ($\text{MNP} = \psi\rho(\psi)$) are 34, 13 and 6 thousand, and are obtained from population sizes of 1,010, 370, and 180 thousand, respectively (Table 3).

Table 2

Estimates of parameters obtained from minimizing the sum of squares of deviations of observed and predicted gross reproductive rates in equation 8, for spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific

γ_0	γ_1	ζ	ψ/ϕ
0.098	0.048	8.0	0.76

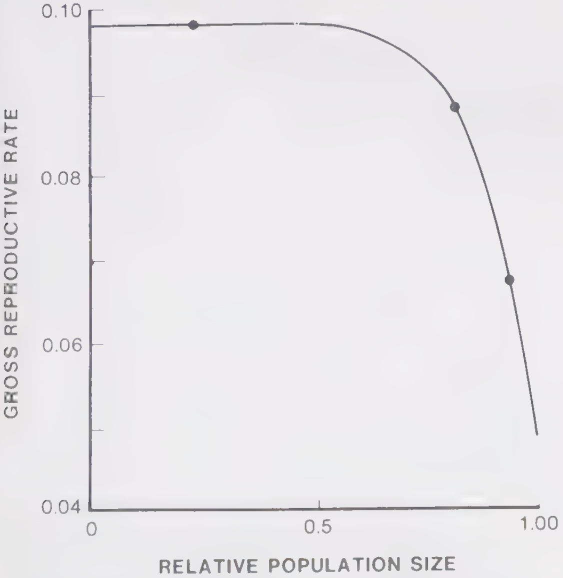

Fig. 3. Observed gross reproductive rates for three spinner dolphin populations versus estimated relative population size, and the estimated gross reproductive rate function from equation 4 obtained by minimizing equation 8

Table 3

Estimates of equilibrium population size, ϕ, for three spinner dolphin populations in the eastern tropical Pacific, with estimates of the maximum net productivity (MNP), and the population size producing MNP (MNPL)

Population	$\hat{\phi}$ (× 1,000)	MNP (× 1,000)	MNPL (× 1,000)
Eastern	1,330	34	1,010
Northern whitebelly	490	13	370
Southern whitebelly	240	6	180

DISCUSSION

The method of estimating MNPL which I describe has possible application to the dolphin populations in the eastern tropical Pacific. The example calculations given for spinner dolphins suggest that MNPL may occur at a relatively high fraction of equilibrium abundance. However, three uncertainties need further attention.

First, the estimates of gross reproductive rate for eastern tropical Pacific dolphin populations are crude because of possible sample biases and analytical biases owing to the methods employed (Smith, 1983; Perrin and Reilly, 1984). The present results must therefore be considered preliminary pending further investigation of the estimates of gross reproductive rate.

A second uncertainty is that only three data points for gross reproductive rate have been used in equation 8 to estimate three parameters. Additional estimates of gross reproductive rate are needed in equation 8; these could be obtained in two ways. The simplest is to assume that other dolphin species have similar reproductive and natural mortality rates at equilibrium and at near-zero population sizes, and similar MNPL values. For instance, there are two populations of spotted dolphin where data are available. A more complex approach to obtaining additional estimates of gross reproductive rate is to use the estimates for each year, rather than the single average over several years, for each population. This approach would require a more complex form for equation 8, where N_0 would be replaced by the population size in the years corresponding to the available annual reproductive rate estimates. The calculations would become rather sensitive to possible time lags in density-dependent

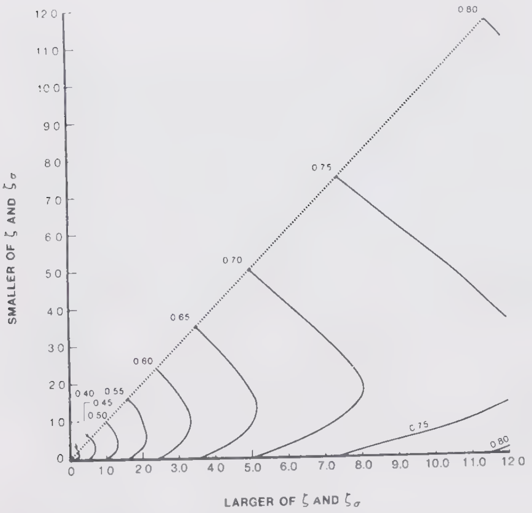

Fig. 4. Population size relative to equilibrium population size (N/ϕ) at which maximum net productivity is obtained (from equation 12) for ranges of values of both shape parameters ζ and ζ_σ.

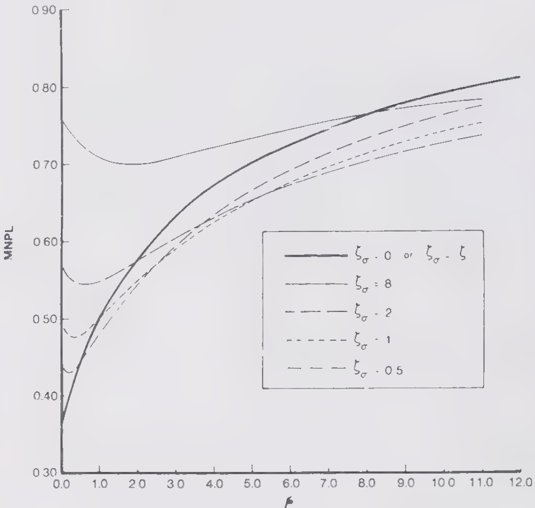

Fig. 5. Maximum net productivity levels (MNPL) versus the value of the shape parameter for changes in gross reproductive rate (ζ), for a series of values of the shape parameter for changes in survival rates (ζ_σ), showing the lack of sensitivity of MNPL to ζ_σ, when ζ is large.

response, but the problem of overparameterization would be minimized.

The third uncertainty in the above estimates of MNPL is that the natural mortality rate is assumed to be constant for all population sizes. This assumption can be explored by replacing μ in equation 3 by one minus the function

$$\sigma(N) = (\sigma_0 - \sigma_1)\left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right) + \sigma_1, \qquad (10)$$

where σ_0, σ_1 and ζ_σ are defined similarly to the corresponding symbols in equation 4. Thus equation 5 is replaced by

$$\rho(N) = (\gamma_0 - \gamma_1)\left(1 - \left(\frac{N}{\phi}\right)^{\zeta}\right) + (\sigma_0 - \sigma_1)\left(1 - \left(\frac{N}{\phi}\right)^{\zeta_\sigma}\right). \qquad (11)$$

Substituting equation 11 for equation 5 in the above development yields expressions parallel to equations 6 and 8. For this model MNPL (ψ) is obtained as the population size N which satisfies

$$\frac{\partial \rho(N)}{\partial N} = 0 = \zeta(\gamma_0 - \gamma_1)\left(\frac{N}{\phi}\right)^{\zeta - 1} + \zeta_\sigma(\sigma_0 - \sigma_1)\left(\frac{N}{\phi}\right)^{\zeta_\sigma - 1}. \qquad (12)$$

This expression is parallel to the calculation used to obtain equation (9), but a similar closed form can not be obtained. The values of MNPL (ψ) from equation 12, assuming $\gamma_0 - \gamma_1 = \gamma_0 - \gamma_1$, are given in Fig. 4, as a contour surface on ζ and ζ_σ. The results are symmetrical in these two parameters and only shown in the first half-quadrant. If $\gamma_0 - \gamma_1 \neq \sigma_0 - \sigma_1$ this surface becomes non-symmetrical.

Values of MNPL for sections through the contour surface in Fig. 4 are shown in Fig. 5, for selected values of ζ_σ. As ζ increases along the abcissa, MNPL first decreases slightly and then increases steadily. MNPL is constrained to a narrowing range for all values of ζ_σ, as ζ increases. For instance, when $\zeta = 8$ in Fig. 5, MNPL ranges from 0.70 to 0.76 when ζ_σ ranges from 0.5 to 8.0. Thus for populations with high MNP levels, the assumption that the natural mortality rate does not change with population size has relatively little effect on the MNPL estimate. Note, however, that estimates of the replacement yield are perhaps greatly affected.

The three uncertainties described suggest several directions which should be followed. Keeping these uncertainties in mind, however, the presently available data for spinner dolphins suggest a rather high value for MNPL, in agreement with Fowler (1981).

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Ammodytoidei: Development and Relationships

E. G. Stevens, A. C. Matarese and W. Watson

THE suborder Ammodytoidei consists of one family, Ammodytidae, with 5 genera and about 18 species. These are small (less than 100–350 mm SL), elongate fish occurring in the littoral and neritic waters of the Atlantic, Indian, Pacific, and Arctic Oceans. Adults form schools but also bury themselves in the sand. They are commercially valuable in the North Sea and off Japan.

The systematic position of Ammodytoidei, reviewed by Duncker and Mohr (1939), is unresolved, although the suborder is considered a perciform derivative by Berg (1940), Greenwood et al. (1966), and Gosline (1971). A second family, Hypoptychidae, has been included in this suborder by these authors and by Robins and Böhlke (1970), but was removed to the suborder Gasterosteoidei by Ida (1976), who considered it a prepercomorph family on the basis of jaw and caudal osteology, egg size, and reproductive behavior (see Fritzsche, this volume).

DEVELOPMENT

The ammodytid genera, *Gymnammodytes, Hyperoplus,* and *Ammodytes* (11 species) are temperate and boreal; *Bleekeria* and *Embolichthys* (7 species) are more tropical in distribution. The confused nomenclature of the North Atlantic species was clarified by the synonomies in Reay (1970) and Russell (1976), where summaries of early life history data were also given. Other larval descriptions were given by Fage (1918) for *Gymnammodytes*; by Altukhov (1978), Kobayashi (1961c), Norcross et al. (1961), Richards (1965), Scott (1972), and Senta (1965) for *Ammodytes*; and by Macer (1967) for North Atlantic species. To date, eggs of 6 species and larvae of 9 species of these genera have been described. No early life history data are available for the tropical genera.

Eggs

Eggs of the six species that have been described are demersal and adhesive, forming clumps on sandy substrates in shallow water. Eggs, probably loosened by tidal currents, have been collected in plankton nets (Williams et al. 1964; Senta, 1965). Russell (1976) summarized studies made on eggs resulting from artificial fertilization. Incubation time ranges from 2.0 to 12.5 weeks. Eggs are irregularly shaped, but generally spherical, from 0.67 to 1.23 mm in diameter, with a single yellow oil globule, 0.17 to 0.42 mm. Embryos develop specific dorsal and ventral pigment, pigmented eyes, a moderate finfold, and pectoral buds prior to hatching at about 3.6 mm.

Larvae

Morphology.—Larvae of Ammodytidae typically are elongate, with rounded snouts which become pointed with age, and preanal length slightly more than 50% body length (Fig. 304). Newly hatched larvae range from 3.0 to 4.6 mm body length. In newly hatched and preflexion larvae the anus does not extend to the edge of the moderately wide finfold but opens to the side. Notochord flexion occurs at 10 to 12 mm body length in most

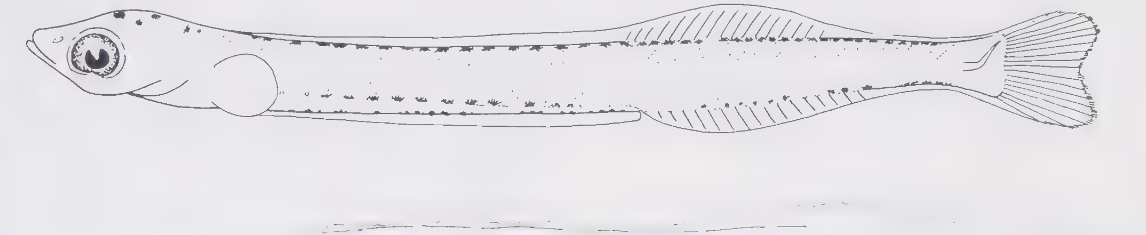

Fig. 304. Larvae of: (upper) *Hyperoplus lanceolatus,* 16 mm, redrawn by H. Orr from Einarsson (1951); (middle) *Ammodytes hexapterus,* 16 mm; and (lower) *Ammodytes marinus,* 16 mm, redrawn by H. Orr from Einarsson (1951).

TABLE 148. SELECTED PIGMENT CHARACTERS OF AMMODYTIDAE LARVAE. 0 = absent, + = present, ↑ = increasing with development, ↓ = decreasing with development, po = posterior, an = anterior.

Species	Stage	Body length (mm)	Head				Ventral gut	Dorsal midline	Caudal	Finfold	Sources
			Jaws	Snout	Brain	Nape					
Gymnammodytes semisquamatus	preflexion	4.8	0	0	0	0	+	0	0	+	Cameron, 1959
	flexion	7.0	0	0	0	+	+	near tail	+	+	Macer, 1967
	postflexion	11.8–38.0	0	+	+, 0	+	+↓	↑+	+	+	
G. cicerellus	preflexion	7.0	0	0	0	+	0	+	+	0	Fage, 1918
	postflexion	11.0–25.0	0	0	+	+	0	↓	+		
Hyperoplus lanceolatus	flexion	6.0	0	0	+	+	+	po 1/3	0	0	Einarsson, 1951
	postflexion	11.0–25.0	0, +	0, +	+	+	+↓	+	↑		Macer, 1967
H. immaculatus	preflexion	5.5–9.0	0	0	0↑	0	an	po 1/4	0	0	Macer, 1967
	flexion	13.0	0	0	+	0	an	↑	+	0	
	postflexion	26.0	+	+	+	0	an	+	+		
Ammodytes tobianus	preflexion	4.0–5.0	0	0	0	+	an	0	0	0	Einarsson, 1955
	flexion	7.5–12.0	0	0	+	+, 0	an	near tail	0	0	Macer, 1967
	postflexion	16.0–27.0	0	0	+, 0	+, 0	0	↑	0↑		
A. marinus	preflexion	4.5–6.0	0	0	0	0	an	0	+	0	Einarsson, 1951
dubius	flexion	7.5–11.0	0	0	+	0	an	po 1/4	+	0	Macer, 1967
americanus	postflexion	19.0–33.0	0	0↑	+	0	+	↑	+		
A. hexapterus	preflexion	7.0–8.0	0	0	0	0	an	0	0	0	Kobayashi, 1961c
	flexion	11.0–13.0	0	+, 0	0	0	an	0	+	0	NWAFC, unpubl.
	postflexion	16.0–31.0	0↑	+	0↑	0	an	0↑	+		

species, and transformation to juveniles occurs at about 40 mm. The caudal fin is the first to ossify, followed by the pectorals, then the dorsal and anal. The median fin rays form in the posterior part of the body, and ossification proceeds forward. During larval development the body thickens somewhat, but maintains its elongate shape. All adult Ammodytidae have protrusible upper jaws, but *Gymnammodytes semisquamatus* is the only species in which this character is reported in larvae as small as 9 mm (Cameron, 1959). Postflexion larvae of *Hyperoplus* develop vomerine teeth which persist in the adult, while *Gymnammodytes* postflexion larvae develop both vomerine and premaxillary teeth which disappear at about transformation. During the larval period *Gymnammodytes, Hyperoplus,* and *Ammodytes* are pelagic. Juveniles and adults are both pelagic and benthic.

Pigment.—Pigment can be a useful diagnostic feature among the larvae of Ammodytidae, especially the location and development of melanophores on the ventral gut margin, the dorsal body margin, and the caudal area, i.e., the tip of the notochord and the edge of hypural elements. These pigment characters are summarized in Table 148. All species have a row of melanophores dorsally on the gut, beginning at or just posterior to the cleithrum, and a postanal row on the ventral body margin from the anus to the tail. The dorsal gut pigment becomes obscured with growth. Specific variations in pigment patterns can be seen in the 16 mm specimens illustrated in Fig. 304. At this length, dorsal midline pigment forms a complete row in *H. lanceolatus,* but occurs only on the posterior quarter in *A. hexapterus* and *A. marinus;* and ventral gut pigment extends the length of the gut in *H. lanceolatus* and *A. marinus* but is found only on the anterior ventral gut of *A. hexapterus.* Pigment patterns of *A. marinus, A. dubius* and *A. americanus* are nearly identical (Macer, 1976) although Richards (1982) has noted differences in the ranges of melanophore numbers, especially on the anterior ventral gut (stomach) and dorsal midline (supradorsal). Pigment appears variously on the head, increasing with age in all species reported. The only reported decrease in pigmentation is on the dorsal and ventral margins of *G. cicerellus* (Fage, 1918). *G. semisquamatus* has pigment on the ventral finfold margin, the only ammodytid species for which finfold pigment has been noted (Cameron, 1959).

Meristics.—Fin ray and vertebral counts for the family Ammodytidae are: Vert 54–78; D 40–69; A 14–36; Pec. 10–16; Pel. 0–I,5; and C 15–17 prin., 13 branched. In all genera the number of precaudal vertebrae exceeds the number of caudal. Robins and Böhlke (1970) report 9+8 principal caudal rays for *Embolichthys sarissa,* but all other ammodytid species, including *E. mitsukurii,* have 8 + 7. *Embolichthys* is the only genus with pelvic fins, which are thoracic. The caudal fin is the first to form, followed by the pectorals, dorsal, and anal. Posterior rays of the median fins form first and development proceeds forward. Fin formation is completed by 30 to 40 mm body length.

RELATIONSHIPS

Although early life history data of the suborder Ammodytoidei do little to clarify its phylogenetic position, larval pigment patterns and myomere-vertebrae counts are useful in separating sympatric species (Macer, 1967). General characters, such as the well developed state of newly hatched larvae and the sequences of fin development, are shared with other perciform derivatives and relatives, but essentially the problem of the systematic position of ammodytids is not yet resolved.

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Notothenioidea: Development and Relationships

E. G. Stevens, W. Watson and A. C. Matarese

NOTOTHENIOIDEA comprises 5 families with 35 genera and about 100 species (Table 140). These familes are endemic to the Antarctic and Subantarctic regions (DeWitt, 1971; Norman, 1938a; Wyanski and Targett, 1981). Adults, ranging from 100 to 900 mm SL, occupy several habitats from the surface to several hundred meters depth and are often associated with continental and island slopes and shelves. Some species are adapted for living close to the undersurface of ice.

Discussions of the systematic position of notothenioids are found in Gosline (1968) and Norman (1938a), who consider them Perciformes or perciform relatives on the basis of the adult cranial osteology; the jugular position of the pelvic fins, which have one spine and five rays; and the caudal fin ray number, usually 14. Both note the reduced number of pectoral radials found in Notothenioidea. Gosline (1968) unites the notothenioids with trachinoids and blennioids using characters such as the one to one ratio of vertebrae to dorsal and anal fin rays, more than 25 vertebrae, and fewer than 15 branched caudal rays. Gosline (1968), Norman (1938a), and other recent workers (i.e., Andersen and Hureau, 1979) separate Nototheniidae and Harpagiferidae making a total of five families (this classification is used here), whereas Nelson (1976) follows Berg (1940) and

Table 141. Notothenioidea: Egg Diameter (mm) and Larval Size at Selected Developmental Stages (mm SL).

Family	Egg diameter	Hatching	Notochord flexion	Juvenile
Bovichthyidae	Unknown	Unknown	Unknown	ca. 25
Nototheniidae	1.2–4.0	6–14	9–20	25–60
Harpagiferidae	2.4–3.0	7–13	ca. 9–13	35–38
Bathydraconidae	1.5–3.0	Unknown	18–24	24–34+
Channichthyidae	2.8–4.5	ca. 14	18–42	50–60+

Table 140. Notothenioidea: General Summary and Early Life History Information.

Family	Number of genera	Approximate number of species	Distribution	Early life history: Descriptions: Genera	Early life history: Descriptions: Species	Early life history: Illustrations: Species
Bovichthyidae	3	12	Antarctic, Subantarctic	0	0	0
Nototheniidae	8	50	Antarctic, Subantarctic	5	16	12
Harpagiferidae	5	15	Antarctic, Subantarctic	2	4	3
Bathydraconidae	10	14	Antarctic	7	8	6
Channichthyidae	11	17	Antarctic	8	8	7

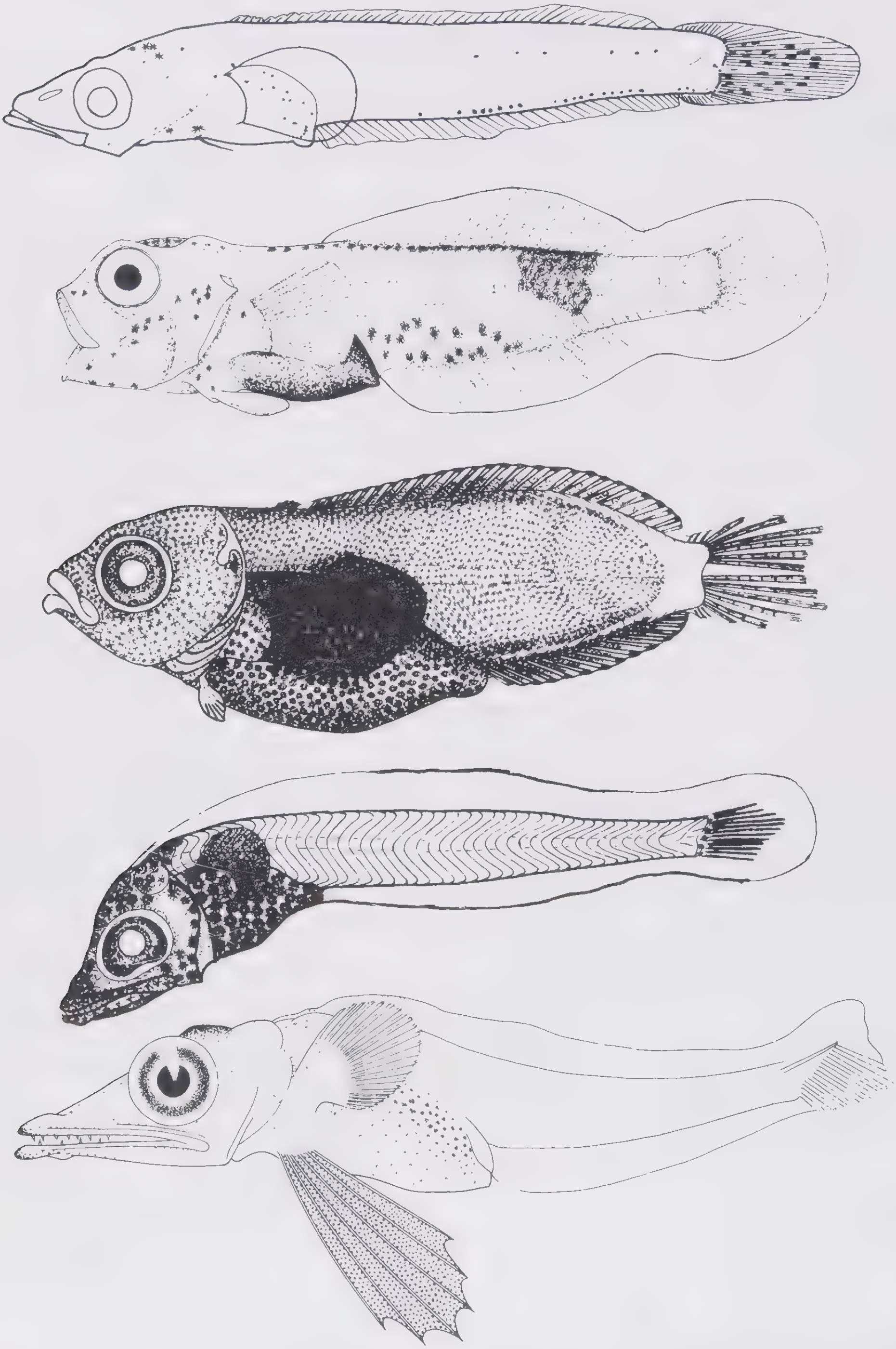

Fig. 301. Notothenioid larvae (from top to bottom): Nototheniidae: *Patagonotothen larseni,* 35 mm, from North and White (1982); Harpagiferidae: *Harpagifer bispinis,* 18.2 mm, from Everson (1968); Harpagiferidae: *Artedidraco mirus,* 24.0 mm, from Efremenko (1983); Bathydraconidae: *Psilodraco breviceps,* 16.9 mm, from Efremenko (1983); and Channichthyidae: *Pagetopsis macropterus,* 19 mm, redrawn by H. Orr from Regan (1916).

TABLE 142. NOTOTHENIOIDEA: SELECTED MERISTICS. Sources listed here do not include the following cited in the text: Andriashev (1959); DeWitt (1970); Norman (1937, 1938); Nybelin (1947, 1951); Regan (1913d, 1916); Yefremenko (1979a, b). Omissions indicate no data were found in the literature. While this paper was in press a revision of the Nototheniidae was published (Anderson, 1984).

Family Genus	Number of species	Fin rays						Vertebrae			Sources
		D_1	D_2	A	Pec.	Pel.	Principal caudal	Pre-caudal	Caudal	Total	
Bovichthyidae											
Bovichthys	10	VII–VIII	18–21	13–19	14–16	I, 4–5				41 (1sp.)	Hureau and Tomo, 1977
Cottoperca	1	VI–VIII	21–24	20–24	17						
Pseudophrites	1–2	VII–VIII	19–20	23–25	18	I, 5					Scott, 1962
Nototheniidae											
Dissostichus	2	VIII–X	25–29	25–30	25–29	I, 5		18–20		54–55	de Ciechomski and Weiss, 1976
Eleginops	1	VIII–IX	24–26	22–24	22–24	I, 5		12	30–31	42–43	de Ciechomski and Weiss, 1976
Pleuragramma	1	VI–VIII	33–38	36–39	20–21	I, 5		18–20		53–55	
Aethotaxis	1	VII	34	30	27–28	I, 5		16	36	52	DeWitt, 1962b
Cryothenia	1	IV–VI	34–36	33–35	24–26	I, 5	14–17	13–18	33–37	50–53	Daniels, 1981
Pagothenia	2	IV–VI	30–37	26–33	23–24	I, 5	14				DeWitt, 1964b
Patagonotothen	16	IV–VIII	27–38	27–37	24–28	I, 5				54–55 (1sp.)	
Notothenia	ca. 27	III–VIII	25–41	21–36	16–30	I, 5	14–16	14–22	27–37	44–58	
Harpagiferidae											
Artedidraco	5	II–IV	24–30	16–21	14–17	I, 5					
Dolliodraco	1	II–III	22–25	14–15	16–18	I, 5		13	21–22	34–35	DeWitt and Tyler, 1960
Histiodraco	1	II–III	26	17	18–19	I, 5					
Pogonophryne	7	II–III	25	16–18	19 (1sp.)	I, 5		15	23	38 (1sp.)	
Harpagifer	1	III–V	21–26	16–21	15–18	I, 5		10–11	24–25	35–36	
Bathydraconidae											
Bathydraco	4	0	34–40	29–31	22	I, 5				52–53	
Gerlachea	1	0	45–47	34–35	26–28	I, 5		25	38	63	
Racovitzia	1	0	30–37	27–31	22–25	I, 5		19–20	32–34	52–54	DeWitt, 1964a
Prionodraco	1	0	34–38	29–33	21–22			16	33–34	49–50	
Cygnodraco	1	0	61–66	35–38	22–23						
Parachaenichthys	2	0	42–46	30–33	21–23						
Psilodraco	1	0	27–30	27–29	25–27			16		48	
Gymnodraco	1	0	28–30	22–26	21–22	I, 5	13	20–21	28	48–50	DeWitt and Tyler, 1960
Akarotaxis	1	0	31–33	27–28	22–23	I, 5	12–13	17	33	50	DeWitt and Hureau, 1979
Vomeridens	1	0	34	32	31–33	I, 5	12	18	36	54	DeWitt and Hureau, 1979; DeWitt, 1964a
Channichthyidae											
Champsocephalus	2	VII–XI	32–41	31–40	22–29	I, 5		16–18		60–64	Kock, 1981
Pagetopsis	2	IX–XV	26–31	24–27	22–23	I, 5		18–20		56–58	
Pseudochaenichthys	1	VIII–XI	28–32	27–31	22–25	I, 5		16–18		51–55	Kock, 1981
Neopagetopsis	1	XIV	34	29	26						
Dacodraco	1	III	32	29	24	I, 5					
Chaenichthys	2	VI–IX	30–35	27–34	18–22	I, 5				54–56	
Chaenocephalus	1	V–IX	37–42	36–40	23–26	I, 5		18–20		60–64	Kock, 1981
Cryodraco	2	III–V	40–45	39–46	23–25	I, 5		20–22		63–65	
Chionodraco	3	V–VII	37–51	33–38	21–24	I, 5		16–18		60–64	
Chaenodraco	1	VI–VIII	38–42	32–35	22–25	I, 4		18–20		60–62	
Chionobathyscus	1										

Greenwood et al. (1966) in placing Harpagiferinae as a subfamily of Nototheniidae (Table 140).

DEVELOPMENT

The first work on the early life history of these fishes was undertaken with material collected on the polar expeditions of the early 20th century. Regan (1916) illustrated larvae of seven notothenioid species. Additional early life history data were sparse until the Antarctic expeditions of the second half of the century. In the last 30 years efforts have been directed toward understanding the biology, ecology, population dynamics, and physiological adaptations of these fish. In these investigations some early life history data have been acquired. Larvae of 36 species have been described (Table 140). The most comprehensive summaries are the key in North and White (1982), the papers of Yefremenko (1979b, c) and the atlas of Efremenko (1983a).[1] No early life history data are available for the family Bovichthyidae except for a brief description of the behavior and an illustration of a 25 mm prejuvenile of *Bovichthys variegatus* (Robertson and Mito, 1979).

Eggs

Eggs of four notothenioid families have been described including some known only from studies of ovaries (Table 141). Eggs are moderate to large (1.2–4.5 mm diameter) with large yolks, no oil globules, and small perivitelline spaces (Marshall, 1953; Andriashev, 1965; Dearborn, 1965). In one species, *Notothenia* (*Trematomus*) *bernacchii,* eggs are bright yellow to deep brown. Most species are demersal spawners; nesting behavior has been observed in *N. bernacchii* (Moreno, 1980) and *Harpagifer bispinis* (Daniels, 1978). However, *Notothenia microlepidota* eggs have been reported from plankton collections (Robertson, 1975a). The demersal eggs are sticky, clinging to substrate or algae. One species, *N. neglecta,* reared in the laboratory from artificially fertilized eggs, has an incubation time of 103–150 days and hatches with a well-developed, heavily pigmented body, black eyes, and a large yolk sac (White et al., 1982). Daniels (1978) reports an incubation time of 14 to 18 weeks for *H. bispinis.*

Larvae

Morphology.—The described larvae of 36 species display some morphological similarity (snout–anus length), and some diversity (snout length and body shape). Preflexion larvae, ca. 6–18 mm SL, are elongate with large pectoral fins and moderate to wide finfolds. Channichthyid larvae have well developed pelvic fins at this stage and more elongate snouts than larvae of other notothenioids. Some species have large yolk sacs which persist after notochord flexion has begun. Preanal lengths range from slightly under to slightly over 50% of body length.

During flexion and postflexion stages most larvae maintain their elongate shape (Fig. 301). However the larvae of the harpagiferid genera *Artedidraco* and *Pogonophryne* become very robust (North and White, 1982; Efremenko, 1983a). Notochord flexion occurs between 9 and 42 mm with larval Harpagiferidae and Nototheniidae flexing at the shortest lengths, Channichthyidae at the longest, and Bathydraconidae at intermediate lengths (Table 141). Size at transformation to the juvenile stage also spans a wide range with *Harpagifer bispinis* settling at 18.3 mm (Everson, 1968) and pelagic larvae of other species reaching 24–60 mm (de Ciechomski and Weiss, 1976; North and White 1982; Yefremenko, 1979b, c).

Larvae of all species develop pelvic fins. Channichthyid larvae retain their elongate snouts and develop teeth and preopercular and rostral spines not reported for other notothenioids (Fig. 301).

Pigmentation.—Pigment patterns of all known larvae are highly specific and are useful identification criteria. The amount and location of pigment varies within families and the amount usually increases with development. A few species have general body pigment, but most exhibit patterns in one or more of the following areas: dorsal body margin, ventral body margin, body midline, peritoneum, gut, and along the myosepta. The occipital and parietal areas typically are pigmented; many species have snout, opercular, and jaw pigment as well. The paired fins are usually pigmented. Pigment is found at the base of the caudal fin in most species, associated with the posterior margin of the hypural elements or the bases of the caudal rays.

Meristics.—Meristics are from counts given for adults by Regan (1913d, 1916), Norman (1937, 1938a), Nybelin (1947, 1951), Andriashev (1959), and DeWitt (1970) (Table 142). Vertebral counts are especially useful diagnostic features within and between families. The dorsal, anal, pectoral, and vertebral counts have been the most significant characters linking larvae to adults (Yefremenko, 1979b, c). The sequence of fin formation is the same in Nototheniidae, Harpagiferidae, and Bathydraconidae with pectoral and caudal fins forming first, followed by pelvics, with dorsal and anal last to ossify. In Channichthyidae the pelvics are precocious and are present in yolk-sac larvae.

RELATIONSHIPS

Knowledge of the early life history of Notothenioidea has not contributed to understanding relationships between Blennioidei and other perciform suborders, but does offer some clues to relationships within the suborder. The lengthy ovarian egg development (Dearborn, 1965; Everson, 1970) is probably related to the cold environment. In other aspects of spawning, i.e., nesting behavior, long incubation time, and laying of demersal adhesive eggs, this infraorder resembles other cold-water blennioids. The well developed state of newly hatched larvae and the sequence of fin development as well as the general lack of specialized larval structures are also blennioid features. Further study of developmental characters, such as the sequence of ossification, might contribute to better understanding of the relationships among the Blennioidei. Superficial morphological and meristic resemblances exist among notothenioid larvae and those of other blennioid species, for example, the notothenioid *Patagonotothen larseni* (Fig. 301), the trachinoid *Trichodon trichodon* (see Trachinoidea, this volume) and the blennioid *Heterostichus rostratus* (see Blennioidea, this volume). As relationships among the blennioids become better known, their relationship with other perciforms might become clearer.

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[1] Efremenko and Yefremenko are alternative transliterations of the name of the same author.

FOOD AND FEEDING OF BOCACCIO (*SEBASTES PAUCISPINIS*) AND COMPARISON WITH PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) LARVAE IN THE CALIFORNIA CURRENT

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ABSTRACT

The composition of the diet of larval bocaccio (*Sebastes paucispinis*) and Pacific hake (*Merluccius productus*) overlapped in copepod types and developmental stages, but important differences were evident from gut content analyses of specimens collected in 1975 CalCOFI cruises. Both bocaccio and Pacific hake larvae have large mouths, but first-feeding bocaccio preyed on smaller organisms than first-feeding hake (30-170 μm wide vs 40-350 μm in hake). Compared with small hake larvae, early stages of bocaccio ingested a greater diversity of food types including larval euphausiids, diatoms, dinoflagellates, tintinnids, and cladocerans. Although copepod nauplii constituted the dominant prey in bocaccio larvae less than 7.0 mm long, there was a total lack of adult copepods and very low incidence of copepodites in the diet. In contrast, adult copepods, primarily calanoids, made up a significant portion of the diet in all sizes of hake larvae examined, contributing about 74% of overall prey volume compared to about 33% in 7-13-mm bocaccio larvae.

Observations of feeding incidence in relation to time of capture suggested a faster rate of gut evacuation in bocaccio larvae.

RESUMEN

La composición del alimento ingerido por las larvas de *Sebastes paucispinis* y *Merluccius productus* abarca similares especies de copépodos adultos y sus fases de desarrollo, pero importantes diferencias fueron observadas en el análisis del contenido estomacal de los ejemplares recolectados durante los cruceros CalCOFI de 1975. Las larvas de *S. paucispinis* y de *M. productus* tienen boca grande. Las larvas de *S. paucispinis* al iniciar su alimentación, capturan organismos más pequeños que las larvas de *M. productus* (30-170 μm de ancho y 40-350 μm de ancho respectivamente). Las larvas más jovenes de *S. paucispinis* ingieren una mayor diversidad de organismos que las larvas de merluza, incluyendo las fases larvales de eufáusidos, diatomeas, dinoflagelados, tintínidos y cladóceros. Aun cuando en larvas de *S. paucispinis* menores de 7 mm de longitud, los nauplios de copépodos constituyeron la presa dominante, hubo una total ausencia de copépodos adultos y escasos copepoditos. En contraste, en las larvas de merluza examinadas los copépodos adultos, principalmente Calánidos constituyeron el 74% del volumen total, comparado con un 33% en las larvas de *S. paucispinis* de 7-13 mm. de longitud.

La incidencia de alimentación en relación con la hora de captura sugiere que las larvas de *S. paucispinis* efectuan una evacuación del tramo digestivo más rapida.

INTRODUCTION

Rockfish (*Sebastes* spp, family Scorpaenidae) larvae are among the most commonly occurring larvae in the California Current; they rank third or fourth in relative abundance in California Cooperative Oceanic Fisheries Investigations plankton surveys, with peak abundance during January and February (Ahlstrom 1961, 1965). Identification of the more than 60 species that occur off California and Baja California is a difficult task, but complete larval series of some important commercial species have been described, including that of bocaccio, *S. paucispinis* (Moser 1967a; Moser et al. 1977). Bocaccio is the most abundant rockfish species in commercial catches from central and northern California (Frey 1971). In southern California this species is important in recreational fisheries: bocaccio constitute 37% of all rockfishes taken on partyboats (Hartman 1980) and rank first or second among rockfish species taken on private boats (Wine 1982; Racine 1982; Ono 1982).

Considerable biological information is available on bocaccio, including age and growth (Phillips 1964), fecundity (Phillips 1964; MacGregor 1970), reproductive biology (Moser 1967a, b; MacGregor 1970), and development and distribution of early life-history stages (Moser 1967a; Moser et al. 1977; Ahlstrom et al. 1978). There are no data, however, on the feeding of bocaccio larvae. Feeding studies of larvae of other major species in the California Current region were reported by Arthur (1976) for northern anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), and jack mackerel (*Trachurus symmetricus*) and by Sumida

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and Moser (1980) and Bailey (1982) for hake (*Merluccius productus*). Bocaccio and other rockfishes differ from many marine fishes in their mode of reproduction. They are highly fecund live-bearers and give birth to larvae that are 4-5 mm long, with functional jaws, eyes, and pectoral fins. In *Sebastes*, the yolk-sac stage occurs within the ovaries, and newborn larvae are equivalent to the first-feeding larvae of oviparous species. As part of a continuing study of the feeding habits of larvae of California Current fishes, this paper summarizes data on stomach contents, mouth size, and feeding incidence of bocaccio larvae.

MATERIALS AND METHODS

Specimens examined in this study consisted of 96 larvae, 4.2-12.8 mm in body length, from 34 formaldehyde-preserved samples collected during the CalCOFI cruises of 1975 (7412, 7501, 7503, and 7505) aboard R/V *David Starr Jordan* and R/V *Alexander Agassiz*. Stations occupied represent an area bounded by 37°16.8′N, 124°19.9′W and 32°40.8′N, 117°52.4′W, approximately off San Francisco Bay south to San Diego, California. Samples were collected with a 505-m-mesh, 1-m aperture plankton net towed obliquely from an approximate depth of 210 meters to the surface.

Procedures for measuring larval body length, mouth width, and for dissecting the gut and identifying stomach contents are discussed in Sumida and Moser (1980). Food volume index was calculated for each food particle by treating copepod eggs as spheres, and nauplii, copepodites, and adults as ellipsoids. Details of the mathematical computations are explained in Sumida and Moser (1980).

RESULTS AND COMPARISONS

Composition of Food

Copepod nauplii were the dominant food items (75%-81%) consumed by bocaccio less than 7 mm long, with calanoid nauplii far outnumbering those of other groups (Table 1). Copepod eggs and eggs of other invertebrates, copepodites, tintinnids, coccoliths, cladocerans, and phytoplankton constituted a minor portion of the diet. Adult copepods were entirely lacking in the guts of larvae less than 7 mm long. Copepodites and adult copepods were found in increasingly greater numbers in larvae longer than 7 mm; however, copepod adults did not become significant prey until the larvae reached 10 mm. Copepod nauplii remained the dominant prey category until the larvae reached 9 mm, and declined thereafter. Of the other diverse categories found in larvae shorter than 7 mm, only invertebrate eggs were found consistently in larger larvae.

Food in bocaccio larvae contrasts with that found in hake larvae, where calanoid adults and copepodites made up the major portion of the diet in all sizes of larvae examined (Sumida and Moser 1980).

Size of Food, Mouth Width

The bulk of food particles ingested by bocaccio larvae less than 8.5 mm long was concentrated in a size range of 50-200 μm, and prey of this size range continued to be a major part of the diet in larvae larger than 8.5 mm (Figure 1). Beginning at about 7 mm, prey sizes up to 400-500 μm appeared in the guts; however, prey items less than 300 μm dominated in the diet even in the largest larvae (Figure 1).

Mouth width was about 0.3 mm at birth, doubled before the larvae reached 6 mm, and doubled again just before the larvae reached 9 mm (Figure 2). Maximum size of prey items ingested by first-feeding bocaccio larvae was about 50% of maximum mouth width, and reached a maximum of 60% in 5-mm larvae (Figure 1). In comparison, maximum prey size was about 90% of maximum mouth width for first-feeding hake larvae, 80% for 4-mm larvae, and about 70% for 5-mm larvae (Sumida and Moser 1980). This reflects dietary differences in first-feeding larvae of the two species; copepod nauplii were the primary constituent in the bocaccio, whereas adult copepods and copepodites composed much of the diet in hake. This is clearly seen in comparisons of the two species' total volumes of major prey items (Table 2). The total volume (in percent) of nauplii consumed by bocaccio larvae in this study was five times that found in hake larvae, whereas the volume (in percent) of adult copepods eaten by bocaccio was less than half that found in hake. Although first-feeding bocaccio larvae have smaller mouths than hake, the rate of increase in mouth width is greater in bocaccio, and mouth size in bocaccio exceeds that of hake at about 7 mm length (Figure 2). Coincidentally, this is also when notochord flexion occurs.

Feeding Incidence

Arthur (1976) defines feeding incidence as the percentage of larvae containing at least one food item in the gut for a given sample. This term refers to presence of food in the gut and does not necessarily reflect recent feeding activity. The plot of feeding incidence of bocaccio larvae at time of sampling shows a diurnal pattern, reaching a maximum from about 0800 to 1600 PST and declining rapidly thereafter (Figure 3). Although the sample size and temporal coverage are limited, the data suggest that bocaccio have a rapid rate of digestion and evacuation after cessation of feeding, compared with hake. This is also evident in plots of the mean food volume index and mean num-

TABLE 1
Food Composition of Bocaccio Larvae

	Size range (mm)																	
	4.0-4.9		5.0-5.9		6.0-6.9		7.0-7.9		8.0-8.9		9.0-9.9		10.0-10.9		11.0-11.9		12.0-12.9	
Food item	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Copepod adults																		
Clausoclanaus sp	—		—		—		—		—		2		—		4		7	
Paracalanus sp	—		—		—		—		2		—		—		3		—	
Oithona sp	—		—		—		2		3		2		31		26		73	
Calanoid	—		—		—		—		—		4		—		—		20	
Total adults	—		—		—		2	1.2	5	3.9	8	2.9	31	43.7	33	31.1	100	45.2
Copepodites																		
Oithona sp	2		11		—		10		2		2		11		5		18	
Calanoid	7		2		1		8		21		3		2		37		23	
Cyclopoid	2		2		—		2		—		—		—		—		—	
Disintegrated/ unidentifiable	4		6		3		—		12		—		4		—		12	
Total copepodites	15	2.4	21	3.9	4	14.8	20	12.0	35	27.1	5	1.8	17	23.9	42	39.6	53	24.0
Copepod nauplii																		
Calanoid	388		334		22		103		70		34		17		11		14	
Cyclopoid	82		78		—		22		6		13		1		3		1	
Harpacticoid	1		1		—		—		—		—		2		—		—	
Disintegrated/ unidentifiable	5		3		—		—		2		3		—		—		—	
Total copepod nauplii	476	75.3	416	77.6	22	81.5	125	75.3	78	60.5	50	18.0	20	28.2	14	13.2	15	6.8
Copepod eggs	21	3.3	6	1.1	—	—	—	—	—	—	212	76.5	1	1.4	—	—	47	21.3
Copepod egg clusters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1.9	—	—
Euphausiid																		
Eggs	—	—	—	—	—	—	3	1.8	2	1.6	—	—	—	—	—	—	—	—
Nauplii	—	—	2	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Calyptopis	2	0.3	—	—	—	—	—	—	—	—	—	—	—	—	1	0.9	1	0.4
Metanauplii	—	—	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	3	1.4
Diatom	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dinoflagellate	1	0.2	3	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tintinnid	7	1.1	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Invertebrate eggs (.14-.26 most .14-.17mm)	79	12.5	66	12.3	1	3.7	14	8.4	8	6.2	2	0.7	2	2.8	14	13.2	—	—
Cladoceran	3	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Salp	—	—	—	—	—	—	1	0.6	—	—	—	—	—	—	—	—	—	—
Coccolith	5	0.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unid. crustacean	3	0.5	1	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unid. particle w/brown chloroplasts	12	1.9	12	2.2	—	—	1	0.6	—	—	—	—	—	—	—	—	2	0.9
Unid. particles	7	1.1	7	1.3	—	—	1	0.8	—	—	—	—	—	—	—	—	—	—
Total no. food particles	632		536		27		166		129		277		71		106		221	
No. larvae examined* ($\Sigma = 96$)	55		19		6		6		3		2		1		1		3	
No. larvae with food ($\Sigma = 66$)	33		17		2		4		3		2		1		1		3	

*None with yolk

TABLE 2
Cumulative Frequency Distribution of Numbers and Volume for Major Prey Types in Bocaccio and Hake Larvae

Prey type	Range max. width (μm)		Mean vol. ($10^6 \mu m^3$)		Frequency of occurrence		Freq. × vol. ($10^9 \mu m^3$)		% of total vol.	
	Bocaccio	Hake	Bocaccio	Hake	Bocaccio	Hake	Bocaccio	Hake	Bocaccio	Hake
Copepod and other invertebrate **eggs**	40-430	50-100	4.270	0.364	475	674	2.028	0.245	14.9	0.7
Copepod **nauplii**	50-370	40-300	3.088	4.013	1210	441	3.736	1.770	27.5	5.3
Copepodites	80-250	80-450	8.752	14.698	212	393	1.855	5.776	13.6	17.4
Copepod **adults**	120-390	110-600	25.202	57.418	179	426	4.511	24.460	33.2	73.8
Other	20-470	40-550	16.424	49.401	89	18	1.462	0.889	10.8	2.7

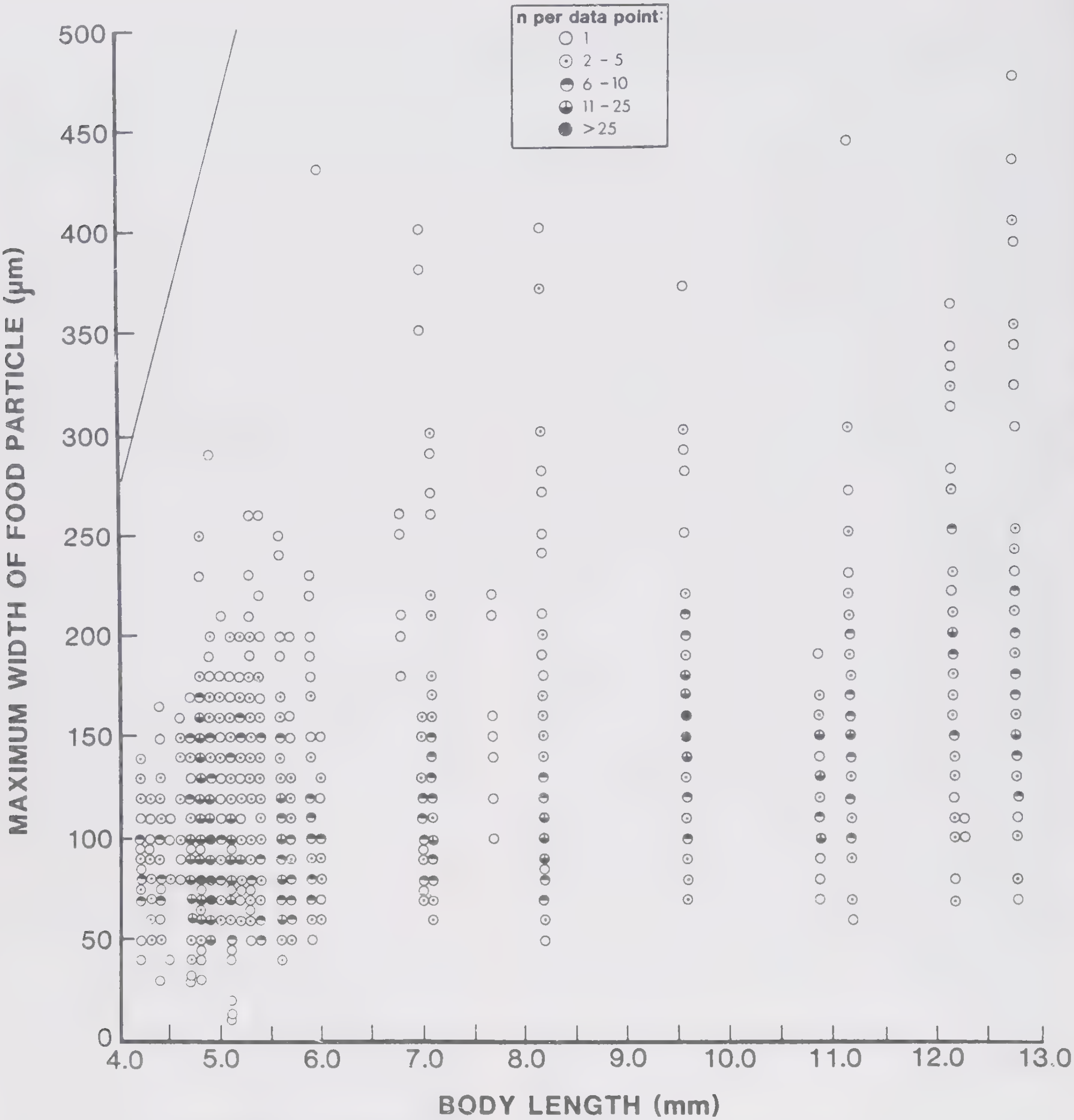

Figure 1. Size of food particles ingested by 66 bocaccio larvae. Oblique line represents maximum mouth width.

ber of food particles (Figure 4). The two plots agree closely except for the single large volume at time 0001-0300. This point represents a single 9.6-mm sample larva (others were empty), which consumed an unusually large number of adult copepods and copepodites.

DISCUSSION

Prey composition in the sample of bocaccio larvae studied is similar to that found in many marine teleosts—a diet dominated by copepod nauplii in the early larval stages, with copepodites and adult copepods becoming increasingly more important in later larval

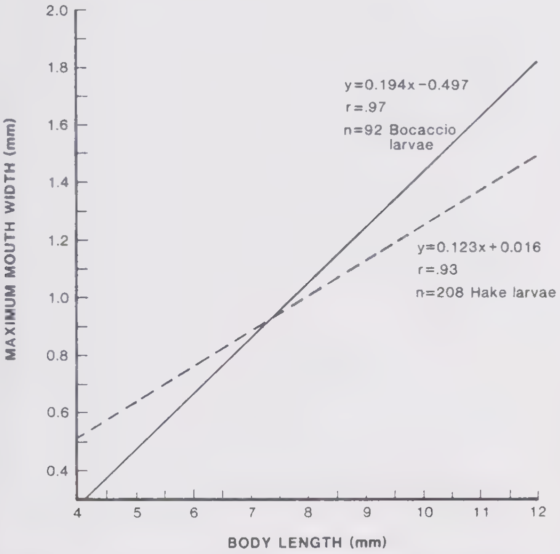

Figure 2. Mouth width of bocaccio (solid line) and Pacific hake (dashed line) larvae

stages (Arthur 1976; Hunter 1981). The maximum size of prey increases with bocaccio larval growth, although small prey are consumed throughout the larval period, during which the minimum prey size changes little. This pattern contrasts with that seen in hake (*Merluccius productus*) larvae, where copepodites and adult copepods were eaten by the smallest larvae and were predominant prey in larvae larger than 4 mm.

Bainbridge and McKay (1968) observed similar contrasting patterns in two north Atlantic species: the redfish (*Sebastes* spp, a congener of bocaccio) and cod (*Gadus morhua*, a relative of *Merluccius*). Copepod eggs and nauplii dominated the diet of redfish, whereas postnaupliar stages predominated in cod. The contrast in feeding patterns may be partly explained by differences in mouth size: mouths are considerably wider in early hake larvae compared with bocaccio, although this relationship is reversed in larvae larger than 7.5 mm (see Figure 2). Another factor may be the depth distribution of larvae of the two species. Ahlstrom (1959) found *Sebastes* spp larvae in the upper mixed layer and thermocline, with an abundance maximum at about 40 m, whereas hake were within and

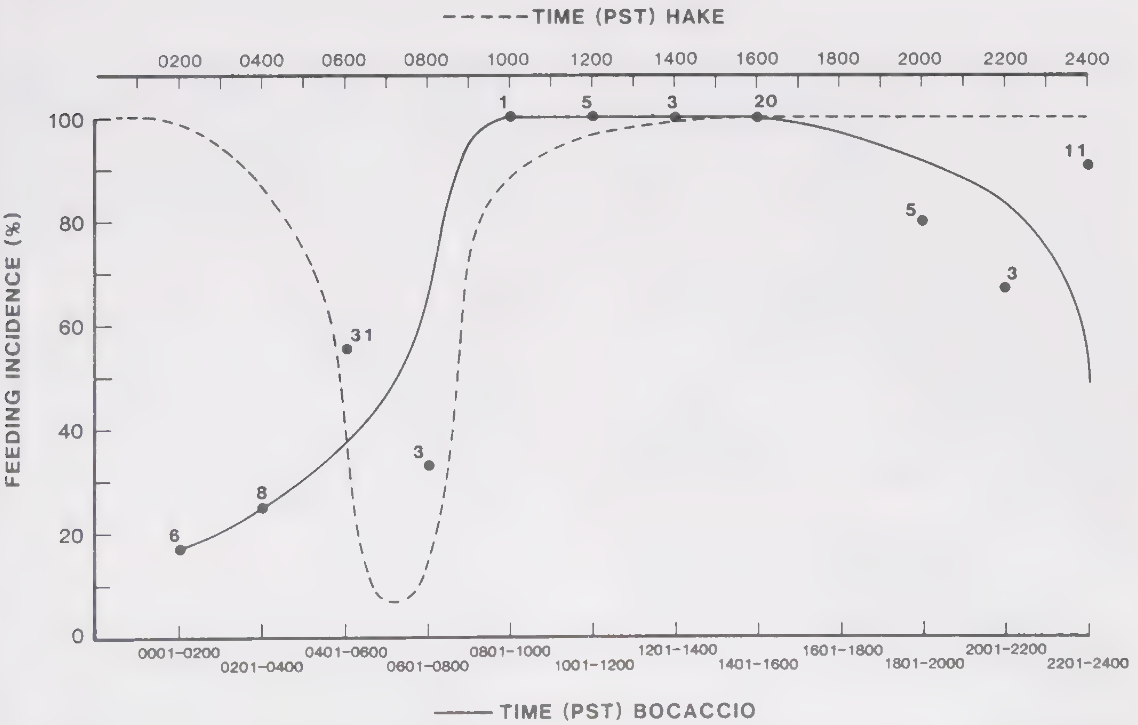

Figure 3. Feeding incidence of bocaccio and Pacific hake larvae at time of capture. Bocaccio data (solid line) grouped in 2-hour intervals, hake data (dashed line) in 1-hour intervals. Values of data points indicate sample size of bocaccio larvae. Curve for hake taken from Sumida and Moser, 1980.

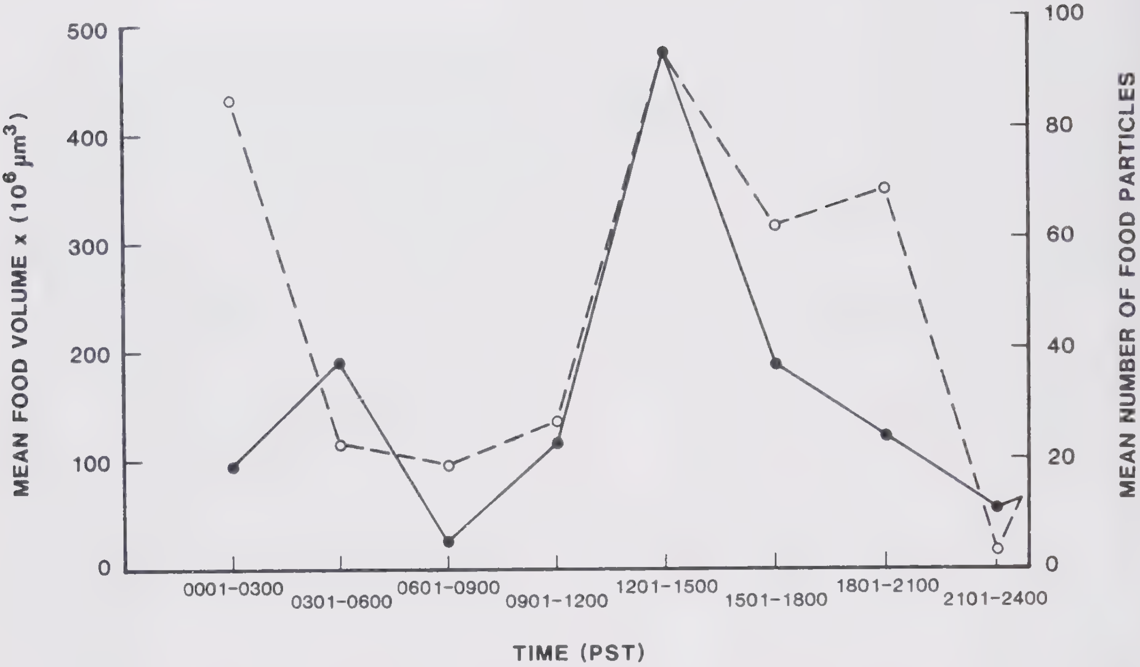

Figure 4. Mean food volume index (dashed line) and mean number of food particles (solid line) of bocaccio larvae. Samples grouped into 3-hour time intervals.

below the thermocline and had a peak abundance at about 70 m. Bailey (1982) examined Ahlstrom's samples of hake larvae for size-related vertical distribution, and found larvae < 8 mm at 50-100-m depth, but larger larvae at greater depths to 300 m. Beers and Stewart (1969) showed a sharp decline in total microzooplankton at about 50 m at several stations off southern California. Although this decline was most marked for tintinnids and other ciliates, it was also evident for naupliar and postnaupliar copepods in the 35-103-μm and > 103-μm size categories. The data suggest that bocaccio are consuming relatively abundant nauplii in their vertical range, while hake are either selecting the larger postnaupliar stages or are capturing them more effectively because their size makes them disproportionately more perceptible at low prey densities.

Arthur (1976) showed a diurnal maximum of feeding incidence in Pacific sardine and northern anchovy, as did Bainbridge and McKay (1968) for redfish and cod. Sumida and Moser (1980) showed that hake reach a peak incidence of 100% at sunset and maintain this until about 0100 hours. Then the incidence declines rapidly until sunrise, when it increases rapidly to 100%. In bocaccio, incidence peaks in midmorning, is maintained at 100% until sunset, then decreases steadily to a minimum at about 0100 hours. Incidence then begins to increase steadily to the midmorning maximum. The contrasting patterns could be explained by an intrinsically faster rate of digestion and evacuation in bocaccio compared with hake. Another possibility is that prolonged high incidence in hake is related to their larger prey size and the lower temperature of their habitat.

ACKNOWLEDGMENTS

We thank Abraham Fleminger (Scripps Institution of Oceanography) for his kind assistance in identifying copepods, Richard Charter (NMFS, Southwest Fisheries Center) for assisting with the CalCOFI larval fish data base, Ken Raymond (NMFS, Southwest Fisheries Center) for drafting figures, and Lorraine Prescott (NMFS, Southwest Fisheries Center) for typing the manuscript.

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Illustrating Fish Eggs and Larvae

B. Y. Sumida, B. B. Washington and W. A. Laroche

SCIENTIFIC illustrations of fish eggs and larvae are an indispensible component of any descriptive work, providing a visual reference of form and structure which is not possible to express by written descriptions and measurements alone. Illustrations facilitate identification by emphasizing distinctive but often subtle morphological characters and allow for comparison of features at different developmental stages and with morphologically similar taxa. These qualities make illustrations the preferred and most frequently used aid for taxonomic identification of fish eggs and larvae.

The broad range of morphological diversity found among larval fishes requires flexibility in technique and style to produce effective illustrations, but the criteria of accuracy, clarity, and consistency of style should be met. The basic concept behind illustrating a fish larva involves accurately representing a three-dimensional, somewhat transparent organism on a two-dimensional sheet while emphasizing characters which are most useful in identifying the actual larva from the drawing. Such characters include the fins, pigmentation patterns, and details of the head such as the jaws, spines and eyes. Internal structures such as myomeres, the gut, cleithrum, and posterior end of the notochord may also be emphasized but without masking important external characters. Details of other internal structures as well as shading or stippling for contrast are best excluded or deemphasized to maintain clarity. Pigmentation is important in identification of most larvae and should be depicted clearly. External melanophores can be drawn with a fine-tipped pen as realistically as possible. Internal pigmentation can be effectively represented by using light stippling with a smaller sized penpoint. Care must be taken to avoid confusion of internal structures with pigmentation.

Specimens selected for illustration should ideally be those of the best condition available and representative of the particular developmental stage in both pigmentation pattern and morphology. The number of specimens to be illustrated is determined by the nature and objective of the publication, the amount of material available in various size groups, and the degree of morphological and pigmentation change undergone by the particular species during ontogeny. Specimens from described series should be archived in a museum collection for proper care and future reference after completion of the illustrations, and catalog numbers should be published.

The detailed drawing begins with an accurate body outline showing the proper body proportions and position of fins and critical pigment spots. This is most easily achieved by drawing in light or blue pencil from a camera lucida-equipped microscope. Other methods include drawing from a projection of a slide transparency of the specimen or tracing a photograph. By convention the lateral view of the larva is drawn, with the head to the left. The exception to this is made with right-eyed pleuronectiforms. In some instances a dorsal or ventral view is also necessary to clarify a pigment pattern or laterally projecting morphological structures. If sketching through a camera lucida, it is helpful to use a magnification which allows the entire specimen to be in the field of vision as long as important details remain visible. Any resulting distortions at the periphery of the field can be compensated for by differentially focusing the microscope on the particular region involved while carefully pencilling along the image, then reconstructing a smooth line where disjointed lines meet. Problems involving specimens that are too large or too small can often be overcome by using lens adapters or eyepieces of lower or higher magnification. Large specimens may require being drawn in sections which are later pieced together. This original sketch should be made large enough to clearly indicate fine details such as the full complement of fin rays, but not excessively so with the result of producing lines which bleed in the final reduction for publication. Related to this is the use of appropriate sizes of pen points which produce lines fine enough to draw minute details yet not be lost in reproduction. Therefore, in determining the original size of each drawing, thought should be given to the desired reduction ratio as well as the number of illustrations comprising each plate. An opaque projector is most useful for obtaining a specific size for the final drawing from the initial sketch, but photocopy reductions also work well. With this final pencilled sketch, the illustrator can work with the larva under a microscope as a reference to complete details of the drawing before attempting to ink it. A light table can be helpful when tracing or inking over a rough pencilled sketch. The illustrator should always have a set of meristics of the specimen being drawn and an understanding o the important characters to be emphasized. A thorough inspection for accuracy is essential to insure agreement between illustrations and descriptive text, especially concerning pigmentation and meristic elements with size and stage of development. Ideally exact counts and measurements can be obtained directly from the illustration, allowing easy identification of the larva.

Illustrations are often designed for comparison of features at different stages of development or for comparison of similar features which occur among different taxa. Special care should be taken to represent similar features in a consistent style from illustration to illustration. For example, a partially ossified fin ray element, an ossified fin ray, and a fin spine may each be depicted in a consistent but slightly different manner so that the illustration not only shows the number and position of fin elements but also the type of element and its relative stage of development.

Literature dealing with larval fishes contains a broad array of illustrative styles, techniques, and quality. Many of these are of limited use since they fail to meet the criteria discussed above. Photographs frequently yield unsatisfactory results due to difficulties in focusing on small, transparent organisms so that all body parts appear equally sharp, and they preclude emphasizing inconspicuous but important features for identification. Color illustrations in a variety of media, although potentially valuable, particularly for xanthophores, are limited due to prohibitive publication costs, poor reproducibility, and the absence of a long-lasting color preservative. Half-tone illustrations (see Ahlstrom, 1965) are effective but difficult to reproduce. These latter two techniques may become more practical with advances in photocopy technology. The preferred technique in widespread use consists of pen and ink drawings done in black india ink. Various styles of illustrations of diverse groups of larvae are represented in Moser (1981) and in this volume which serves as a useful overview. Poul Winther, George Mattson, and other artists (Ahlstrom and Ball, 1954; Ahlstrom and Counts, 1955; Bertelsen and Marshall, 1956; Ege, 1953, 1957, and 1958; Grey, 1955b; Moser, Ahlstrom and Sandknop, 1977; Moser and Ahlstrom, 1970; Tåning, 1961; Richardson and Washington, 1980) have been instrumental in establishing a fine style of pen and ink drawings which we emulate and have found most effective in its applicability to larval fish identification. We maintain a degree of flexibility in technique and style which varies with the taxonomic group under consideration but falls within the general framework discussed above.

Illustrating a fish egg poses a more difficult problem than illustrating a fish larva and will be limited to a brief discussion. Encapsulation by the chorion necessitates representing the three-dimensional quality of the egg in the drawing while showing important morphological and pigmentation characters of internal structures (Ahlstrom and Moser, 1980; Matarese and Sandknop, this volume) with as much clarity as possible. Difficulties arise due to the superimposing of these characters from a two-dimensional perspective, particularly when the chorion is ornamented, when an oil globule(s) is present, and when the developing embryo is fully coiled.

In spite of the more complex structural representation required, the same criteria of accuracy, clarity and consistency of style apply to egg illustrations. The relative proportions of the egg size to the size of the embryo, oil globule(s), and width of perivitelline space, the number of myomeres, and length of gut need to be accurately drawn. An effective balance between showing important characters for identification and three-dimensional realism of the egg is required to maintain clarity. Several illustrations of the egg at different stages of development and from different perspectives are helpful in demonstrating key characters such as embryonic pigmentation, myomeres, and position of the oil globule(s) in the yolksac. Adherence to a consistent illustrative style is primarily critical for a developmental series of eggs. As with fish larvae, pen and ink drawings provide the most practical technique for illustrating fish eggs, but the specific style of illustrating and details shown depend upon the character of the egg and its stage of development. Many kinds of illustrative styles and techniques are found in the literature (see Ahlstrom and Moser, 1980 and references cited therein) and examination of these is most helpful in effectively illustrating a particular type of fish egg.

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COMPARATIVE QUALITY OF ROTIFERS AND COPEPODS AS FOODS FOR LARVAL FISHES

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ABSTRACT

The rotifer *Brachionus plicatilis* and the copepod *Tigriopus californicus* are easily cultured and commonly used as foods for larval fishes. Sizes of rotifers, nauplii, and copepodites, ranging in width from 74 to 221 μm, were related to their weight, volume, and caloric content. Between the smallest and largest size classes—a width increase of two times—rotifer dry weight increased from 0.10 to 0.47 μg/animal, and naupliar dry weight increased from 0.04 to 0.38 μg/animal. An individual rotifer contained more calories than a nauplius of the same width even though the organic tissue fraction of the rotifers had a lower caloric value (4.8 cal/mg) than that of the copepods (5.9 cal/mg). *Tigriopus* nauplii weighed less per unit width and contained more ash than rotifers. These width-specific differences in caloric content should be considered in any bioenergetic study in which rotifers and copepod nauplii are used as foods.

RESUMEN

El rotífero *Brachionus plicatilis* y el copépodo *Tigriopus californicus* son de fácil cultivo y son frecuentemente utilizados como alimento para larvas de peces. Las dimensiones transversales de los rotíferos, nauplios y copepoditos oscilan entre 74 y 225 μm. Estas tallas fueron relacionadas con el peso, volumen y valor calorico respectivo en cada grupo. Entre las tallas más pequeñas y las mayores, si la anchura se duplica, el peso seco de los rotíferos aumenta de 0.10 a 0.47 μg, y el de los nauplios de 0.04 a 0.38 μg por ejemplar. Un rotífero contiene más calorías que un nauplio del mismo ancho, aunque la fraccíon de tejido orgánico del rotífero tiene un valor calórico inferior (4.8 cal/mg) que en los copépodos (5.9 cal/mg). Los nauplios de *Tigriopus* pesaron menos por unidad de anchura y produjeron más cenizas que los rotíferos. Estas diferencias en valor calórico específicas en relación a la dimensión transversal de los organismos, debiera ser consideradas en las estimaciones bionergéticas, cuando rotíferos y nauplios son utilizados como alimento.

INTRODUCTION

In studies of larval fish energetics, it is necessary to know dry weights and caloric values of prey items. We have determined these values for the rotifer *Brachionus plicatilis* and for the nauplii and copepodites of *Tigriopus californicus*, a harpacticoid copepod, as part of a study on effect of diet on growth of larval northern anchovy, *Engraulis mordax*. Rotifers are widely used as food for larval fish in laboratories (Theilacker and McMaster 1971; Solangi and Ogle 1977; Fontaine and Revera 1980; Hunter 1981); harpacticoid copepods are an important food for many larval fish in the field (Mason 1974; Arthur 1976; Schmidt-Moser and Westphal 1980) and are also used as prey in laboratories (Kinne 1977; Kahan et al. 1982; Hunter MS[1]). We cultured *Brachionus* using the methods of Theilacker and McMaster (1971), and *Tigriopus* using the technique followed at the Southwest Fisheries Center, La Jolla, California.

Copepod biomass has been determined with several methods and expressed in different units (Table 1). Copepod total length and prosome length have been used as predictors for both dry and wet weight of Formalin-preserved adults (Pertsova 1967; Grusov and Alekseyeva 1970; Durbin and Durbin 1978; Feigenbaum 1979), Formalin-preserved copepodites (Mullin and Brooks 1967; Durbin and Durbin 1978), and Formalin-preserved nauplii (Durbin and Durbin 1978). Yet width is the dimension that limits fish larvae's selection of prey (Beyer 1980; Hunter 1981), and width is also a more accurate predictor of copepod wet weight than is length (Pearre 1980). Because copepods lose weight when preserved in Formalin (Ahlstrom and Thrailkill 1963; Omori 1970, 1978), and the dry weight lost varies among species (Omori 1970, 1978; Durbin and Durbin 1978), a width-weight relation for fresh samples is needed. Fresh dry weights available for copepods have been related to length (Comita et al. 1966) and to stage (Paffenhöfer 1971), or they have been given as a mean weight for a composite sample of field-collected nauplii and copepodites (Houde and Schekter 1981). The fresh dry weights reported for

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[Manuscript received February 9, 1984.]

[1] Hunter, J.R. Synopsis of culture methods for marine fish larvae. Presented at the Ahlstrom Memorial Symposium, La Jolla, California, August 1983. Manuscript

TABLE 1

Copepod Weight and Caloric Data

			Predictor of weight weight = 1-dry; 2-wet; 3-carbon weight				
	Life stage[1]: 1-naup; 2-cop; 3-cop-V; 4-adults; 5-mixed	Fresh sample	Length	Stage	Caloric content	Ash content	Reference
Individual species							
Acartia clausi	1;2;4	–	1	1	–	–	Durbin & Durbin 1978
Acartia tonsa	1;2;4	–	1	1	–	–	Heinle 1966
Calanus cristatus	3;4	–	1;2	1;2[2]	–	+	Omori 1970
Calanus finmarchicus	3;4	+	–	1	+	+	Comita & Schindler 1963
Calanus finmarchicus	3;4	+	1	1	+	–	Comita et al. 1966
Calanus helgolandicus	5	+	–	–	+	–[3]	Slobodkin & Richman 1961
Calanus helgolandicus	1;2;4	+	–	3	–	–	Mullin & Brooks 1970a; 1970b
Calanus helgolandicus	1;2;4	+	–	3	–	–	Paffenhöfer 1971
Calanus pacificus	1	+	–	3	–	–	Fernandez 1979
Centropages typicus	2	–	–	1;3	+	+	Razouls 1977
Rhincalanus nastus	2	–	1;3	–	–	–	Mullin & Brooks 1967
Rhincalanus nastus	2	+	–	3	–	–	Mullin & Brooks 1970a
Temora stylifera	2	–	–	1;3	+	+	Razouls 1977
Tigriopus californicus	5	+	–	–	+	–[3]	Slobodkin & Richman 1961
Individual genus							
Pseudocalanus	1;2;4	–	1	1;3	+	+	Corkett & McLaren 1978[4]
Many species treated individually							
	4	–	1	–	–	–	Conover 1959
	3;4	+	–	1	–	–	Conover 1960
	2;4	–	2	2	–	–	Pertsova 1967
	2;4	–	2	2	–	–	Krylov 1968
	3;4	–	2	2	–	–	Grusov & Alekseyeva 1970
	1;2;4	?	–	1	–	–	Hargrave & Geen 1970
	4	–	–	–	+	+	Laurence 1976
	3;4	+	1;3	–	–	+	Omori 1978
	1;2	+	1	–	–	–[3]	Breteler et al. 1982
Unidentified copepods or mixed samples							
	5[2]	+	–	–	–	–	Beers 1966
	5	–	1	–	–	–	Feigenbaum 1979
	5[5]	+	–	–	–	–	Houde & Schekter 1981
	5[6]	–	–	–	-	–	Hanson et al. 1982

[1] Cop = copepodite; cop-V = stage V copepodite
[2] Copepod carbon content is given as a percentage of dry weight
[3] Ash content is corrected for, but not given
[4] Review paper
[5] Copepod dry weight is related to mesh size used for sample (see text)
[6] Mean dry weight is given

rotifers (Theilacker and McMaster 1971; Doohan 1973; Eldridge et al. 1977) were given as averages for laboratory populations, and they do not reflect size-specific weight.

Not only is dry weight lower after Formalin preservation, but significant amounts of carbon and nitrogen are also lost from copepod tissues (Durbin and Durbin 1978; Omori 1978). Thus, calorimetric measurements are most accurately performed on fresh samples. Calorimetric values are available for fresh samples of adult calanoid copepods (Slobodkin and Richman 1961; Comita and Schindler 1963; Comita et al. 1966) and adult harpacticoids (Slobodkin and Richman 1961). No information was available on the width-specific dry weight and caloric content of fresh samples of rotifers, copepod nauplii, and copepodites that are commonly used as foods for larval fishes.

METHODS

Preparation of Rotifers

We harvested rotifers from cultures and placed them overnight in a one-liter cylinder containing seawater and algae. This procedure allowed debris to settle and insured that the rotifers were in a good nutritional state when sampled. Thus the nutritional characteristics of the rotifers when dried and weighed should be comparable to their state when used as food. We siphoned debris-free rotifers through a series of nitex screens (ranging in size from 44 μm to 194 μm), retaining samples in which the major component was animals of a single width class (Table 2). Pure samples (n = 3) were obtained for the 74-110 μm rotifer width class, but the other sieved samples (n = 25) were slightly contaminated by rotifers from adjacent size classes. For these samples, an aliquot was counted to estimate total numbers (the coefficient of variation for the aliquots was between .17 and .20) and numbers belonging to each width class. Next, we poured a volume containing 2,500-5,000 animals (usually about 30 ml) onto a preweighed Nucleopore filter (Durbin and Durbin 1978). To eliminate salt crystals, we rinsed the samples with 30 ml of isotonic ammonium formate (3.4%), which sublimates when heated, leaving no residue. Blanks of seawater and ammonium formate were run through filters and used to correct the final weights.

We estimated width-specific dry weight of the rotifers belonging to the three slightly contaminated width classes by using a multiple regression ($y = a_1x_1 + a_2x_2 + a_3x_3$) in which y was the total dry weight of the sample, x_1, x_2, and x_3 were the relative frequencies of the width classes, and a_1, a_2, and a_3 were the width-specific average dry weights (Draper and Smith 1966). We used the midpoint of the width range for the four width classes and corrected the total weight for the frequency of eggs, assuming egg weight was the same as the weight of the smallest rotifer, 0.10 μg, which agrees with an unpreserved egg weight of 0.092 μg determined for the same species by Doohan (1973).

Preparation of Copepods

Copepods were difficult to sieve because the appendages of the live animals caught on the mesh of the nets. Thus carapace width was not the limiting factor in sieving. We found that anesthetizing the animals with dilute MS222 (0.06% MS222 in seawater) relaxed the appendages and permitted more effective sieving. The anesthetized animals were quickly revived in sea water. We rinsed sieved animals in ammonium formate solution and hand sorted them to width classes (Table 2) on a slide, forming nauplii and copepodites into piles of 200 to 400 animals. We sieved and sorted 10 copepod samples. Five of the sorted samples were composed of a single size (width) class, and the remaining samples were of two size groups. To estimate size-specific weights for copepods, we followed the same multiple regression procedure used for rotifers.

TABLE 2
Prey Characteristics

		Per individual		
Prey	Width class μm	Dry[1] weight μg (SE)	Volume $\times 10^6 \mu m^3$	Caloric value $\times 10^{-3}$ cal
Brachionus plicatilis (4.4 cal/mg)[2]				
Rotifers	74-110	0.10 (.01)	0.65	0.44
	110-147	0.22 (.04)	1.73	0.97
	147-184	0.41 (.06)	2.96	1.80
	184-195	0.47 (.08)	3.99	2.07
Tigriopus californicus (4.9 cal/mg)[2]				
Nauplii	74-110	0.04 (.01)	0.20	0.20
	110-147	0.13 (.01)	0.55	0.64
	147-184	0.25 (.01)	1.17	1.23
	184-195	0.38 (.00)[3]	1.77	1.86
Copepodites				
	147-184	0.63 (.15)	3.38	3.09
	184-221	1.20 (.26)	6.21	5.88

[1] Regression coefficients are used for average dry weights.
[2] Caloric value for total tissue dry weight; see text.
[3] <0.01

We placed slides of copepods and Nucleopore filters with rotifers in a 60°C oven and dried them overnight to constant weight (Lovegrove 1966). We then removed the piles of copepods from the slides by using a single-edged razor blade and weighed the copepod samples, as well as the rotifer samples with filters, on a Cahn electrobalance to ± 2 μg.

Calculation of Rotifer and Copepod Volumes

Rotifers and nauplii have similar length-width ratios, but they differ in body form and thus in volume. We approximated rotifer volumes as ellipsoids, naupliar volumes as oblate spheroids (dorsoventrally compressed spheres), and copepodite volumes as the sum of a dorsoventrally compressed and elongated ellipsoid (for the prosome or cephalothorax) plus a cylinder (for the urosome or abdomen). After measuring each dimension of individual animals (n = 30 for each width class) to find the relative ratios of the dimensions, we calculated volumes using the midpoint of the width range (Table 2).

We used a Phillipson oxygen microbomb calorimeter to measure caloric content; samples weighed from 2 to 4 mg. Ash was estimated by incinerating dried specimens at 525°C overnight. We hand sorted about 10,000 nauplii and 1,000 copepodites for each calorimetric and ash determination.

RESULTS AND DISCUSSION

Rotifer Dry Weight and Caloric Value

Rotifer dry weight estimates range between 0.10 and 0.47 μg, depending on body width (Table 2). To compare these estimates with the fresh dry weights of *B. plicatilis* given as averages for laboratory populations (Theilacker and McMaster 1971; Doohan 1973; Eldridge et al. 1977), we calculated an average weight using the width-specific weights determined in this study and Theilacker and McMaster's (1971) width-frequency information. The calculated average weight, 0.20 μg, was similar to the average weight of 0.16 μg reported by Theilacker and McMaster (1971). Doohan (1973) also obtained a mean individual dry weight of 0.158 μg. The estimate given by Eldridge et al. (1977) was 0.905 μg, twice the weight of rotifers in our largest width class (Table 2). They observed a large number of egg-bearing females in their samples and did not adjust for egg weight, which may partially explain this weight difference.

We used ash content of 7.8 ± 2.0% dry weight in our expressions of ash-free caloric content (Table 3). Watanabe et al. (1983) give data for *B. plicatilis* from which we calculated a somewhat lower ash content (5.32 ± 1.83% dry weight, $n = 2$). Theilacker and McMaster's (1971) estimated caloric value for *Brachionus* was 5.3 ± 0.1 cal/mg ash-free dry weight, and we found a caloric value of 4.8 ± 0.3 cal/mg ash-free dry weight (Table 3). This variation in ash-free caloric values may simply reflect differences in ash content. Apparently, weight and caloric content among *Brachionus* cultures maintained at the La Jolla laboratory have varied slightly over the years.

TABLE 3
Caloric and Ash Values

	n	% ash	(SD)	n	Calories/mg ash-free dry wt.	(SD)
Brachionus plicatilis						
Rotifers	7	7.8[1]	(2.0)	3	4.8	(0.3)
Tigriopus californicus						
Nauplii	2	16.2	(3.5)	3	5.8	(0.5)
Copepodites	2	17.0	(1.4)	2	6.0	(0.4)
Adults	2	7.3	(0.9)	2	5.9	(0.4)

[1] Theilacker and McMaster, 1971.

Copepod Dry Weight and Caloric Value

Naupliar dry weights ranged from 0.04 to 0.38 μg, and the weight increase was nearly proportional to the cube of the width. Copepodites weighed 2.5 to 3 times a nauplius of corresponding width (Table 2). Average dry weights given in Houde and Schekter (1981) for sieved samples of nauplii and copepodites were 0.15 μg per animal for the 53-110 μm fraction and 0.51 μg per animal for the 110-280 μm fraction. These width-weight estimates appear similar to ours (Table 2), but they are difficult to compare because the size component collected by sieving is not necessarily delimited by the sieve sizes used.

Assuming no between-culture differences, we averaged the caloric and ash values for each of the three copepod stages. The average caloric content of the organic fraction of *Tigriopus* adults and the young stages is similar, about 5.9 cal/mg (Table 4), and comparable to the 5.5 cal/mg reported for *Tigriopus* by Slobodkin and Richman (1961) and to the 5.6 cal/mg average for seven calanoid copepods given by Laurence (1976). (Laurence's values may be low because he used Formalin-preserved samples.) The value we

TABLE 4
Parameters (SE) for Nonlinear Equations ($y = a\,x^b$) for Estimating Rotifer or Copepod Dry Weight (y)[1] from Width, and Linear Equations ($y = a + bx$) for Estimating Dry Weight from Volume

		Width[2]			Volume[3]		
Prey	n	a	b	r^2	a	b	r^2
Brachionus plicatilis							
Rotifers	4	1.4×10^{-5} (2.1×10^{-5})	2.00 (0.29)	.970	0.029 (.033)	0.116 (.013)	.977
Tigriopus californicus							
Nauplii	4	9.2×10^{-8} (6.6×10^{-8})	2.90 (0.14)	.997	— —	— —	—
Nauplii and copepodites	6	— —	— —	—	0.020 (0.13)	0.189 (0.004)	.998

[1] y = dry weight (μg).
[2] x = width (μm).
[3] x = volume × 10^6 μm^3.

sed to estimate caloric equivalents of individual prey Table 2) is based on total tissue dry weight, i.e., rganic plus ash weight, and is less for young stages ecause they have a relatively high inorganic (ash) ontent (Table 3). Young copepod stages have a higher sh content than the adults because the carapace imparts the greatest proportion of the ash weight, and the atio of carapace weight to tissue weight is larger for mall organisms. Our data also showed that females arrying egg sacs contained more ash than non-eggbearing females and males (10.4% as compared to 7.3%), presumably because of the increased numbers of embryos in the sample. Razouls (1977) found the sh-free caloric value was higher for copepodites than dults, but her values are for preserved specimens and may not be comparable.

Regressions of dry weight (*y*) and body width (*x*) gave a good fit for both rotifer and nauplii data (Figure 1); estimates of the parameters for the dry weight and body width equations are given in Table 4. Although the dry weight (*y*) is subject to sampling error because it was estimated from a multiple regression (see Methods), its use to produce the dry weight and body width equations should be of little concern because the errors were negligible (Table 2). The equations given in Table 4 can be used to predict rotifer and naupliar dry weight from measurements of body width. We did not include an equation for the copepodites because we had only two points, but it is clear that at any given width a copepodite has a greater dry weight and caloric content than a rotifer, and a rotifer has a higher dry weight and caloric content than a nauplius.

Rotifer and Copepod Volumes

Zooplankton biomass is often estimated using volume approximations (reviewed by Beers 1976), and the relations between copepod wet weight and volume are summarized by Pearre (1980). Because prey volumes are relatively easy to measure and have been used in feeding studies of marine fish (Sumida and Moser 1980), we related our dry weight measurements to estimated volumes and included equations for predicting dry weight for a given volume (Tables 2 and 4; Figure 2).

Copepod stages have a higher dry weight (and caloric content) than rotifers of the same volume (Figure 2). This may be due to unlike water content or to unlike densities, owing in part to dissimilarities in the weight or composition of their respective integuments. The average ash content of nauplii and copepodites was 16.2% and 17.0% as compared to rotifers, which had an assumed ash content of 7.8% (Table 3).

CONCLUSIONS

For any given width, rotifers have a higher caloric content than *Tigriopus* nauplii. First-feeding fish eating the smallest rotifers get twice as many calories per bite as they do eating *Tigriopus* nauplii of the same width (Table 2). Many first-feeding fish larvae select prey from the smallest size classes, yet older larvae eat prey belonging to all size classes. As a result, variation in estimated daily consumption by larval fish may be caused in part by the differences between the weight estimate for the average prey item and the actual weight of the item eaten. Clearly, an error in estimating food consumption can also result from

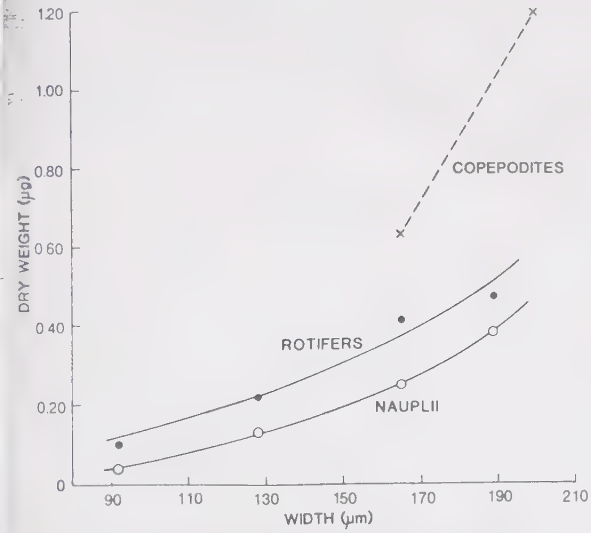

Figure 1. Relations between dry weight (µg) and body width (µm) for the rotifer *Brachionus plicatilis* and the copepod nauplii of *Tigriopus californicus*. Estimates of parameters for equations are in Table 2.

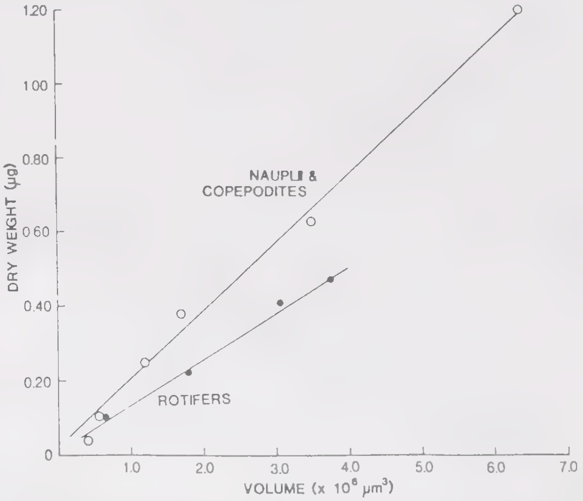

Figure 2. Relations between dry weight (µg) and volume of the rotifer *Brachionus plicatilis* and copepod *Tigriopus californicus*. Estimates of parameters for equations are in Table 2

ignoring specific differences in caloric content among prey organisms.

Regressions of the width-weight measurements can be used to predict the dry weight of rotifers and nauplii of known width. The copepod width-weight model probably cannot be used for weights of calanoid life stages because calanoid nauplii are shaped more like an ellipsoid and thus would weigh more than dorsoventrally compressed harpacticoid nauplii of corresponding width. The copepod volume-weight model may be applicable to calanoid life stages.

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BIOLOGY, DISTRIBUTION, POPULATION STRUCTURE, AND PRE-EXPLOITATION ABUNDANCE OF SPINY LOBSTER, PANULIRUS MARGINATUS (QUOY AND GAIMARD 1825), IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

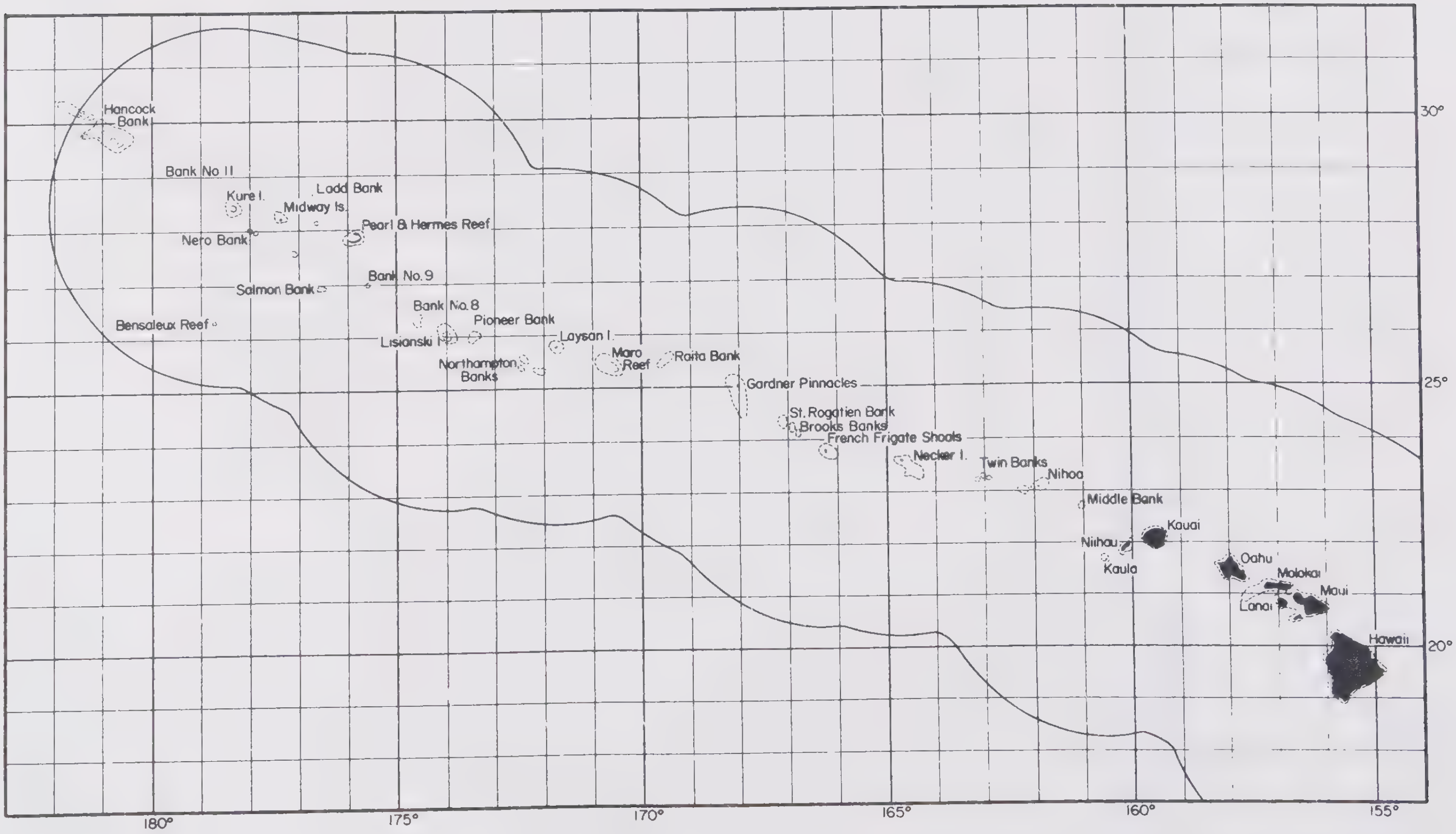
This overview incorporates results of studies conducted on the spiny lobster, *Panulirus marginatus* (Quoy and Gaimard 1825), resource in the Northwestern Hawaiian Islands by the Honolulu Laboratory from October 1976 to September 1981. Of 26 sites surveyed, only Necker Island and Maro reef appeared to have sufficiently large stocks for commercial exploitation. Included also are data on historical catches and fishery development, and results of analyses on geographic and depth distributions, pre-exploitation abundance, size composition, sex ratio, size at maturity, reproduction, behavior, and morphometry. Extrapolation of results from the assessment of the stock at Necker Island provided estimates of the maximum sustainable yield of spiny lobster for the entire Northwestern Hawaiian Islands.

Discussions on economics, fishery potential, and management guidelines are also presented.

spiny lobster
biology
abundance
Northwestern Hawaiian Islands
population structure
distribution

INTRODUCTION

Before 1976, little was known about the marine resources of the Northwestern Hawaiian Islands (NWHI) (Figure 1) and, except for a few commercial fishermen who used French Frigate Shoals as a fishing base or those who made periodic fishing trips for bottomfish, these resources were virtually untouched by humans.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Bank No 11
Kure I.
Ladd Bank
Midway Is.
Pearl & Hermes Reef
Nero Bank
Bank No. 9
Salmon Bank
Bank No. 8
Bensaleux Reef
Pioneer Bank
Lisianski I.
Laysan I.
Northampton Banks
Maro Reef
Raita Bank
Gardner Pinnacles
St. Rogatien Bank
Brooks Banks
French Frigate Shoals
Necker I.
Twin Banks
Nihoa
Middle Bank
Kauai
Niihau
Kaula
Oahu
Molokai
Lanai
Maui
Hawaii

Figure 1. The Hawaiian Archipelago, including the Northwestern Hawaiian Islands

The sequence of events that led to the investigation of the marine and terrestrial resources of these islands is documented in Uchida et al. (1980) and Grigg and Pfund (1980).

From October 1976 to September 1981, the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service conducted resource surveys in the NWHI, concentrating on those species of economic significance and high development potential. The objectives of these surveys were to investigate the unfished waters of the NWHI to determine the species that were available, to define their distribution and abundance, to make a first estimate of their potential yield, and to provide preliminary estimates of the likely catch rates. Among the species that showed excellent potential for development was the spiny lobster, *Panulirus marginatus*.

Thus studies were undertaken to determine the geographic and depth distribution, fecundity and spawning, growth and movement, behavior, population structure, and population dynamics of the spiny lobster. Also studied were predation on spiny lobsters, gear competition, and ghost fishing. The results of these surveys form the basis of this overview report. Results of many of the experiments and individual studies are included in published and unpublished reports of the Honolulu Laboratory.

MATERIALS AND METHODS

The data for this study were obtained from trapping operations of research and charter cruises. The standard gear used was the California two-chambered lobster pot. Because fish traps were also used during the surveys, and because lobsters were also taken by these traps, data from fish trapping stations are also included. Both the pot and trap had identical entrances; however, several pots and traps with modified entrances were used for special studies. The lobster pot and fish trap are described in detail in a forthcoming fishery atlas of the NWHI by R.N. Uchida and J.H. Uchiyama.

On our first cruise (TC-76-06), lobster pots and fish traps were alternated on a string. Each lobster pot was separated from the fish trap by 5 m; each pair of trap-pot combination was spaced 18 m apart. Only two pairs of trap-pot combination were used per string with six strings making up the set at each station.

On subsequent cruises, usually eight lobster pots, spaced 35 m apart, were attached to one string and up to five strings were set at varying depths between 20 and 91 m (10 and 50 fathoms); the pots were occasionally set as shallow as 4 m (2 fathoms). For fish traps, usually four traps were placed on a string and up to five strings set at each station. Depths varied from 9 to 337 m (5 to 75 fathoms).

Occasionally, special large-entrance lobster pots were set as deep as 183 m (100 fathoms) to determine whether large lobsters ($>$140-mm carapace length, CL) were in deeper water and also to examine the spiny lobster's depth distribution. At some stations, fish traps were set singly to depths of 329 m (180 fathoms) to evaluate the catchability of fishes of the snapper-grouper complex; the data obtained from these stations were used to define the spiny lobster's depth limits.

Trapping stations were occupied from about 1800 to 0800 thereby allowing the pots and traps to soak for about 14 hours.

Because almost nothing was known about the distribution of spiny lobsters in time and space (various habitats), preliminary surveys were conducted to identify the most promising sites within the NWHI. A search for suitable depth and bottom conditions was required to make the most efficient use of gear and fishing time. Stations were selected by using existing navigational and bottom contour charts; where information was lacking, bathymetric profiles were first obtained with the echo sounder.

The sampling scheme was modified, after analysis of data from the preliminary surveys, to increase the efficiency of later surveys. The area around each island, bank, and atoll was subdivided into smaller grids or equal-area sampling units 0.1° of latitude and longitude, and within each grid, fishing stations were stratified, whenever possible, by depth. Although some sets were made in waters less than 18 m, sampling was usually confined to the inner shelf (18 to 36 m), outer shelf (36 to 45 m), and shelf edge (45 to 90 m). Some sets were also made in the slope zone (90 to 360 m).

Records were usually kept of the number of legal, sublegal, male, female, and ovigerous female lobsters caught. For most of the lobsters, missing appendages, carapace length, weights, and whether or not the female bore spermatophores (mated) were also recorded. When catches were large or when time was limited, only the total number and weight caught were recorded and the catch was subsampled for lenghts and weights.

For this study, effort is defined as a pot-night for the lobster pot and a trap-night for the fish trap, that is, one pot or one trap fishing overnight, usually for 14 or more hours.

RESULTS

Taxonomy

The spiny lobsters, a clearly defined group in the order Decapoda, can be distinguished from the true lobsters by the lack of claws and the presence of a subcylindrical spiny carapace. In Hawaiian waters, two species of spiny lobsters are found around the major islands -- *P. marginatus* and *P. penicillatus*. Although the species may sometimes be confused with one another, there are distinguishing features that easily separate the two. In *P. marginatus*, the anterior border of the carapace is armed with a pair of strong prominent frontal horns above the eyes, whereas in *P. penicillatus*, there are two pairs of strong anterior spines on the antennal plate (McGinnis, 1972).

Panulirus marginatus is endemic to the Hawaiian islands (George and Holthuis, 1965) and Johnston Atoll (Brock, 1973). *Panulirus penicillatus*, the most widely distributed Indo-Pacific *Panulirus* species, is found from the Galapagos Islands in the east to the Red Sea in the west (Holthuis, 1947).

Historical Catch and Fishery Development

Before the fishery expanded to the NWHI, spiny lobsters were mostly caught around the major Hawaiian islands. The catches were small and constituted only an insignificant part of the total marine fish and shellfish landings in the state. In 1961-75, the mean annual catch reported to the Division of Aquatic Resources, Hawaii Department of Land and Natural Resources, was 3 metric tons (MT) or less than 1 percent of the state's total marine production; however, it is believed that large numbers of lobsters are also taken by recreational fishermen, who are not required to report their catches. The magnitude of the recreational catch has never been determined.

The principal gears used in the commercial fishery around the major Hawaiian islands are tangle nets which are set primarily for spiny lobster, and fish traps (lobsters caught in these traps are considered incidental). About 82 percent of the lobster catch was made in waters around Oahu (Morris, 1968).

The spiny lobster fishery in the NWHI began in November 1976 when one vessel began fishing commercially at Necker Island. In 1977, four other vessels participated in the fishery. The vessels fished primarily at Nihoa and Necker Island but effort was also expended at French Frigate Shoals and as far north as Maro Reef. The principal gear used in this fishery was the California two-chambered lobster pot, a small (0.9 m x 0.6 m x 0.4 m), easy-to-handle, rectangular pot, which occupies about a third as much space as a conventional Hawaiian fish trap.

By 1977, the spiny lobster catch in Hawaii had risen from less than 3 MT in 1976 to slightly more than 37.5 MT (Figure 2). Annual landings in subsequent years fluctuated widely as vessels entered and left the fishery. Because there was no management plan for lobsters during the early years of the fishery, many catches went unreported. Therefore, the catches shown in Figure 2 for 1977-82 were estimated from data collected by NMFS and DAR observers on vessels or from the weight of frozen tails landed (Skillman and Ito, 1981).

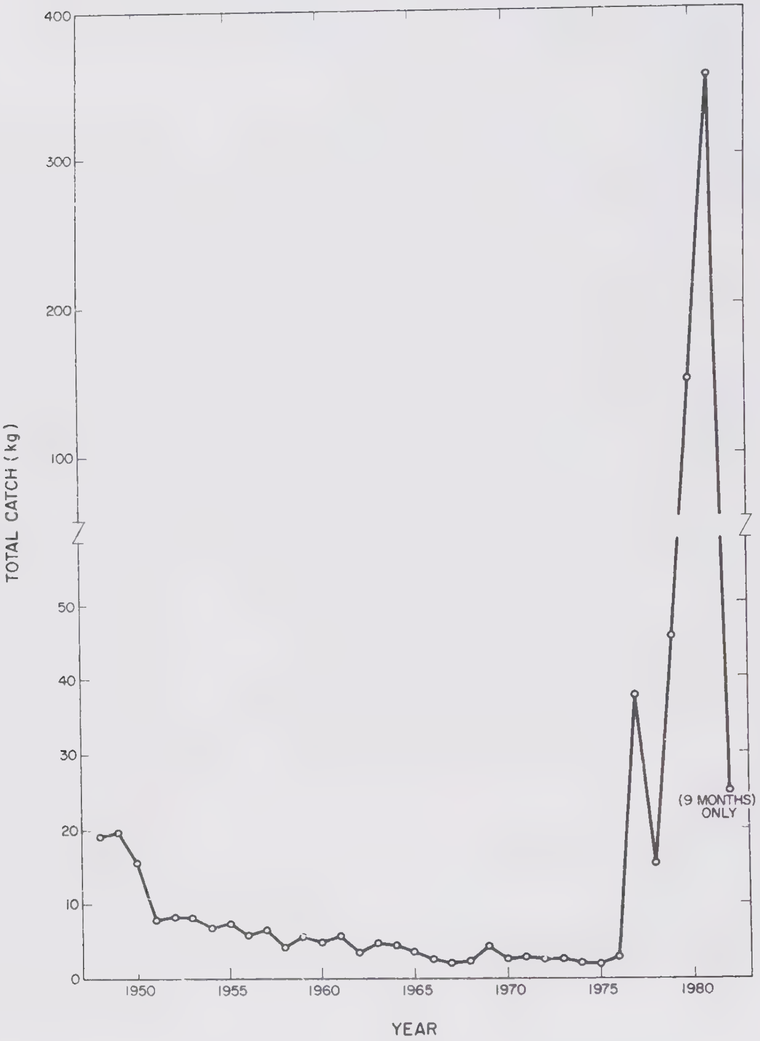

Figure 2. Catch of spiny lobsters in the Hawaiian Archipelago. Data for 1948-78 are from Skillman and Ito (1981); data for 1979-82 are from R.A. Skillman, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, (1983: personal communication).

Geographical Distribution and Pre-exploitation Abundance

Although two species of spiny lobsters occur in waters of the NWHI, they are distinctly separated by depth, unlike their distribution in waters of the main islands where they are found together. *P. penicillatus*, being a shallow-water inhabitant in the NWHI, were never caught in the area of operation, which included all offshore waters from about 18 m and deeper (except at Maro Reef and those islands northward where it was possible to occupy stations in waters less than 18 m deep).

In the NWHI, sampling for *P. marginatus* began at Nihoa, where lobster trapping surveys produced maximum catches of 2.7 individuals/pot-night and 1.84 individuals/trap-night along the southeastern part of the bank (grid 230617) (Table 1 and Figure 3). Nihoa, because of its close proximity to Honolulu, was one of the first lobster grounds in the early years when commercial fishing began in 1976. *P. marginatus* was also found on an isolated bank (henceforth referred to as Nihoa West Bank) near Nihoa, but the catches here were relatively small. Bank 3, a small bank located between Nihoa and Necker, was also visited but no evidence of lobster was found.

Moving northwestward to Necker Island, dense aggregations of *P. marginatus* were found over much of the northern and southern parts of the bank. Catch rates of lobsters in some of the areas reached as high as 13.25 individuals/pot-night (grid 236646) and 25.83 individuals/trap-night (grid 236647). Commercial operations in late 1976 and 1977 produced catches averaging 5-7 individuals/pot-night. The catch rate reached 6.62 individuals/pot-night in 1976 but dropped to 4.83 individuals/pot-night by 1977 and continued a downward trend to 3.32 in 1978, 1.88 in 1979, 1.70 in 1980, and 1.09 in 1981. The fish trap catch rate was 6.18 individuals/trap-night in 1976, 3.32 in 1977, 3.97 in 1978, 5.09 in 1979, 1.82 in 1980, and 5.62 in 1981. The rise in the fish trap catch rate in 1979 and 1981 was due primarily to sublegal lobsters (<77.0 mm CL), which made up 70 to 80 percent of the catch. Because commercial operations significantly reduced the abundance at Necker by the end of 1979, when total catch reached an estimated 45,372 kg, data only for 1976-78 were regarded as indicative of pre-exploitation abundance.

Northwest of Necker Island, *P. marginatus* was also found at French Frigate Shoals, Brooks Banks, St. Rogatien Bank, Gardner Pinnacles, and Raita Bank; however, nowhere was it as abundant as at Necker. The pre-exploitation abundance of *P. marginatus* was extremely low at French Frigate Shoals, Brook Banks, and St. Rogatien Bank, and the species was not caught in fish traps set at Bank 7. Abundance varied at Gardner Pinnacles; some areas (grids 245680, 246681, and 251682) along the southwest and northwest edges of the bank produced relatively good catches. Because the bank at Gardner Pinnacles is extremely large (about 50 nmi in the north-south direction and 24 nmi at the widest point in the east-west direction), about half of it remains unsurveyed. Only one grid at Raita Bank showed relatively high catches.

TABLE 1. CATCH OF LOBSTERS (LEGAL-SIZED, SUBLEGAL-SIZED, AND BERRIED) IN LOBSTER POTS AND FISH TRAPS DURING RESEARCH AND CHARTER CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976 TO SEPTEMBER 1981

Location	Grid		Lobster Pot Catches						Total	Catch/ Pot Night
			1976	1977	1978	1979	1980	1981		
Middle Bank (22° 42'N, 161° 02'W)	227	610	--	0(40)	--	--	--	--	0(40)	0.00
Nihoa (23° 03'N, 161° 55'W)	230	617	--	--	108(40)	--	--	--	108(40)	2.70
	230	619	--	40(40)	--	--	--	--	40(40)	1.00
	231	619	--	107(98)	--	--	--	--	107(98)	1.09
	232	618	--	--	--	--	--	0(32)	0(32)	0.00
		Total	--	147(138)	108(40)	--	--	0(32)	255(210)	1.21
Nihoa West Bank (22° 58'N, 162° 14'W)	229	621	--	--	15(40)	--	--	--	15(40)	0.38
	229	622	--	48(80)	--	--	--	--	48(80)	0.60
	229	623	--	--	--	--	--	0(26)	0(26)	0.00
	230	621	--	98(98)	--	--	--	--	98(98)	1.00
		Total	--	146(178)	15(40)	--	--	0(26)	161(244)	0.66
Bank 3 (23° 13'N, 163° 09'W)	231	631	--	--	--	--	--	0(7)	0(7)	0.00
	232	631	--	--	--	--	--	0(24)	0(24)	0.00
		Total	--	--	--	--	--	0(31)	0(31)	0.00
Necker Island (23° 34'N, 164° 42'W)	232	642	--	--	308(80)	--	--	--	308(80)	3.85
	232	643	--	246(40)	--	--	--	27(28)	273(68)	4.01
	233	644	--	21(40)	--	--	--	--	21(40)	0.52
	233	645	--	4(40)	--	--	--	--	4(40)	0.10
	233	646	--	142(100)	--	--	--	--	142(100)	1.42
	234	643	--	--	--	--	--	--	--	--
	234	644	--	--	--	--	34(24)	--	34(24)	1.42
	234	645	--	220(101)	--	--	--	9(8)	229(109)	2.10
	234	646	--	319(102)	--	--	--	--	319(102)	3.13
	235	645	--	--	186(48)	--	--	--	186(48)	3.88
	235	646	--	395(100)	--	--	15(30)	--	410(130)	3.15
	235	647	1(12)	1,892(337)	--	0(1)	--	--	1,893(350)	5.41
	235	648	96(20)	593(70)	--	--	--	34(23)	723(113)	6.40
	236	645	157(22)	796(98)	--	--	--	151(135)	1,104(255)	4.33
	236	646	160(8)	687(133)	183(40)	301(143)	518(279)	17(25)	1,812(628)	2.88
	236	647	93(6)	710(138)	13(40)	--	--	--	816(184)	4.43
	236	648	24(4)	738(101)	--	86(62)	--	--	848(167)	5.08
		Total	477(72)	6,763(1,400)	690(208)	387(206)	567(333)	238(219)	9,122(2,438)	3.74
French Frigate Shoals (23° 46'N, 166° 18'W)	236	660	--	12(40)	--	--	--	--	12(40)	0.30
	236	662	--	1(40)	--	--	--	--	1(40)	0.02
	236	663	--	--	--	--	--	--	--	--
	237	662	--	7(60)	--	--	--	--	7(60)	0.12
	237	663	--	--	97(80)	0(22)	--	--	97(102)	0.95
	238	662	--	--	--	--	--	8(48)	8(48)	0.17
	238	663	--	16(99)	7(40)	3(23)	--	--	26(162)	0.16
	238	664	--	--	--	--	--	--	--	--
	239	662	--	--	--	--	--	--	--	--
	239	663	--	--	--	--	--	--	--	--
		Total	--	36(239)	104(120)	3(45)	--	8(48)	151(452)	0.33
Brooks Banks (24° 05'N, 166° 50'W)	240	668	--	--	--	3(8)	13(48)	--	16(56)	0.28
	241	667	--	--	--	--	--	--	--	--
	241	668	--	--	--	6(32)	3(32)	--	9(64)	0.14
	241	669	--	--	--	25(32)	--	--	25(32)	0.78
	242	669	--	--	--	5(8)	2(40)	--	7(48)	0.14
		Total	--	--	--	39(80)	18(120)	--	57(200)	0.28
St. Rogatien Bank (24° 25'N, 167° 15'W)	242	670	--	--	--	--	--	--	--	--
	242	671	--	41(59)	--	--	--	--	41(59)	0.70
	243	670	--	--	--	--	5(24)	--	5(24)	0.21
	243	671	--	--	--	--	10(55)	--	10(55)	0.18
	244	671	--	--	--	--	7(39)	--	7(39)	0.18
		Total	--	41(59)	--	--	22(118)	--	63(177)	0.36
Bank 7 (24° 36'N, 167° 18'W)	246	672	--	--	--	--	--	--	--	--
Gardner Pinnacles (25° 01'N, 167° 59'W)	244	679	--	--	26(16)	--	--	--	26(16)	1.62
	245	680	--	--	--	--	--	74(32)	74(32)	2.31
	246	681	--	--	37(16)	--	--	--	37(16)	2.31
	247	681	--	--	--	--	--	--	--	--
	248	681	--	--	23(29)	--	--	--	23(29)	0.79
	249	682	--	--	--	--	42(24)	54(32)	96(56)	1.71
	250	679	--	28(58)	--	--	--	--	28(58)	0.48
	250	680	--	--	--	--	--	0(7)	0(7)	0.00
	250	682	--	--	--	--	53(24)	38(24)	91(48)	1.90
	250	683	--	--	--	--	--	--	--	--
	251	681	--	--	--	--	19(23)	--	19(23)	0.83
	251	682	--	--	152(30)	--	--	--	152(30)	5.07
	252	680	--	--	--	--	--	--	--	--
	252	681	--	--	--	--	12(8)	--	12(8)	1.50
		Total	--	28(58)	238(91)	--	126(79)	166(95)	558(323)	1.73

Note: (N) = trap-nights

TABLE 1. CATCH OF LOBSTERS (LEGAL-SIZED, SUBLEGAL-SIZED AND BERRIED) IN LOBSTER POTS AND FISH TRAPS DURING RESEARCH AND CHARTER CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976 TO SEPTEMBER 1981 (continued)

Location	Grid		Lobster Pot Catches						Total	Catch/ Pot Night
			1976	1977	1978	1979	1980	1981		
Raita Bank	254	694	--	--	--	--	16(40)	--	16(40)	0.40
(25° 35'N, 169° 35'W)	254	696	--	5(22)	--	--	--	--	5(22)	0.23
	255	693	--	137(40)	--	--	--	--	137(40)	3.42
	255	694	--	--	21(24)	--	--	--	21(24)	0.88
	255	695	--	--	--	--	37(32)	--	37(32)	1.16
	256	693	--	--	--	--	40(47)	--	40(47)	0.85
	256	694	--	--	6(6)	--	17(31)	16(32)	39(69)	0.56
	256	695	--	--	--	--	35(23)	--	35(23)	1.52
		Total	--	142(62)	27(30)	--	145(173)	16(32)	330(297)	1.11
Maro Reef	252	704	--	825(151)	--	--	--	--	825(151)	5.46
(25° 29'N, 170° 35'W)	252	706	--	613(99)	96(48)	--	--	--	709(147)	4.82
	253	704	--	50(16)	--	--	--	--	50(16)	3.12
	253	707	--	--	--	--	--	12(24)	12(24)	0.50
	253	708	--	409(142)	--	--	--	--	409(142)	2.88
	254	706	--	69(18)	--	--	65(12)	--	134(30)	4.47
	254	707	--	166(52)	151(48)	--	--	188(64)	505(164)	3.08
	254	708	--	--	--	--	131(48)	59(23)	190(71)	2.68
	254	709	--	--	--	25(16)	--	--	25(16)	1.56
	255	705	--	--	--	--	49(26)	--	49(26)	1.88
	255	706	--	161(47)	--	--	--	--	161(47)	3.42
	255	707	--	--	--	--	145(32)	--	145(32)	4.53
	255	708	--	--	--	90(16)	123(32)	--	213(48)	4.44
	255	709	--	--	--	--	--	--	--	--
	256	706	--	--	--	--	--	--	--	--
	256	707	--	144(40)	--	--	--	--	144(40)	3.60
		Total	--	2,437(565)	247(96)	115(32)	513(150)	259(111)	3,571(954)	3.74
Northampton Seamounts	254	724	--	--	--	--	3(40)	--	3(40)	0.08
(25° 18'N, 172° 04'W)										
Laysan Island	256	717	--	40(24)	--	--	--	--	40(24)	1.67
(25° 42'N, 171° 44'W)	257	716	--	41(24)	--	--	--	--	41(24)	1.71
	257	717	--	91(81)	--	--	--	--	91(81)	1.12
	257	718	--	97(24)	--	--	--	--	97(24)	4.04
	258	715	--	1(10)	--	--	--	--	1(10)	0.10
	258	716	--	120(56)	--	4(40)	0(24)	--	124(120)	1.03
	258	717	--	42(24)	--	--	--	--	42(24)	1.75
	258	718	--	116(64)	27(40)	9(23)	--	--	152(127)	1.20
		Total	--	548(307)	27(40)	13(63)	0(24)	--	588(434)	1.35
Pioneer Bank	259	735	--	--	0(24)	--	--	--	0(24)	0.00
(26° 00'N, 173° 25'W)										
Lisianski Island	258	738	--	--	--	0(16)	--	--	0(16)	0.00
(26° 02'N, 174° 00'W)	259	737	--	--	--	0(40)	--	--	0(40)	0.00
	259	738	--	--	--	--	--	--	--	--
	259	739	--	0(24)	--	--	--	--	0(24)	0.00
	259	741	--	3(24)	--	--	--	--	3(24)	0.12
	260	738	--	4(64)	--	--	--	--	4(64)	0.06
	260	739	--	--	--	--	0(4)	--	0(4)	0.00
	260	740	--	2(4)	--	--	0(4)	--	2(8)	0.25
	261	739	--	0(23)	--	--	--	--	0(23)	0.00
	262	741	--	0(40)	--	--	--	--	0(40)	0.00
		Total	--	9(179)	--	0(56)	0(8)	--	9(243)	0.04
Bank 8	262	745	--	--	0(24)	--	--	--	0(24)	0.00
(26° 17'N, 174° 34'W)	263	745	--	--	--	0(32)	--	--	0(32)	0.00
		Total	--	--	0(24)	0(32)	--	--	0(56)	0.00
Salmon Bank	269	763	--	--	--	--	--	--	--	--
(26° 56'N, 176° 28'W)	269	764	--	2(47)	--	--	0(40)	--	2(87)	0.02
		Total	--	2(47)	--	--	0(40)	--	2(87)	0.02
Pearl and Hermes Atoll	277	757	--	25(40)	--	--	--	2(24)	27(64)	0.42
(27° 48'N, 175° 51'W)	277	758	8(12)	3(24)	--	--	--	0(24)	11(60)	0.18
	277	759	--	25(24)	--	--	7(64)	2(24)	34(112)	0.30
	277	760	--	--	--	--	--	0(22)	0(22)	0.00
	278	757	--	29(24)	--	9(23)	--	2(16)	40(63)	0.63
	278	759	--	16(11)	--	--	6(4)	--	22(15)	1.47
	278	760	--	120(64)	--	119(62)	2(4)	--	241(130)	1.85
	279	757	--	9(24)	--	--	--	4(32)	13(56)	0.23
	279	758	--	6(22)	--	--	--	--	6(22)	0.27
	279	759	--	--	--	8(23)	--	--	8(23)	0.35
		Total	8(12)	233(233)	--	136(108)	15(72)	10(142)	402(567)	0.71
Nero Seamount	279	779	--	--	--	--	0(24)	--	0(24)	0.00
(27° 57'N, 177° 58'W)										

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Location	Grid		Lobster Pot Catches						Total	Catch/ Pot Night
			1976	1977	1978	1979	1980	1981		
Midway Islands	281	774	--	16(30)	--	--	--	--	16(30)	0.53
(28°12'N, 177°22'W)	282	772	--	1(8)	--	--	--	--	1(8)	0.12
	282	773	--	158(88)	166(40)	52(16)	--	--	376(144)	2.61
	282	774	--	111(61)	124(39)	34(23)	--	--	269(123)	2.19
	283	773	--	--	--	--	--	--	--	--
	283	774	--	0(15)	--	--	--	--	0(15)	0.00
		Total	--	286(202)	290(79)	86(39)	--	--	662(320)	2.07
Kure Atoll	283	782	--	--	--	--	0(4)	--	0(4)	0.00
(28°25'N, 178°25'W)	283	783	--	26(96)	20(40)	--	0(4)	--	46(140)	0.33
	284	782	--	101(81)	--	--	--	--	101(81)	1.25
	284	783	--	11(23)	--	--	31(8)	--	42(31)	1.35
	285	783	--	--	--	--	--	--	--	--
		Total	--	138(200)	20(40)	--	31(16)	--	189(256)	0.74
Ladd Seamount	284	766	--	--	--	--	--	--	--	--
(28°32'N, 176°40'W)	285	766	--	--	--	--	0(40)	0(48)	0(88)	0.00
		Total	--	--	--	--	0(40)	0(48)	0(88)	0.00
Bank 11	288	795	--	--	--	--	--	--	--	--
(28°53'N, 179°38'W)	289	795	--	--	--	--	--	--	--	--
		Total	--	--	--	--	--	--	--	--
SE Hancock Seamount (29°47'N, 179°04'E)	298	790	--	--	--	--	--	--	--	--
NW Hancock Seamount (30°16'N, 178°43'W)	302	787	--	--	--	--	--	--	--	--

Location	Grid		Fish Trap Catches						Total	Catch/ Trap Night
			1976	1977	1978	1979	1980	1981		
Middle Bank (22°42'N, 161°02'W)	227	610	--	0(16)	--	--	--	--	0(16)	0.00
Nihoa	230	617	--	--	35(19)	--	--	--	35(19)	1.84
(23°03'N, 161°55'W)	230	619	--	5(16)	--	--	--	--	5(16)	0.31
	231	619	--	--	--	--	--	--	--	--
	232	618	--	--	--	--	--	--	--	--
		Total	--	5(16)	35(19)	--	--	--	40(35)	1.14
Nihoa West Bank	229	621	--	1(16)	--	--	--	--	1(16)	0.06
(22°58'N, 162°14'W)	229	622	--	2(20)	--	--	--	--	2(20)	0.10
	229	623	--	--	--	--	--	--	--	--
	230	621	--	--	--	--	0(1)	--	0(1)	0.00
		Total	--	3(36)	--	--	0(1)	--	3(37)	0.08
Bank 3	231	631	--	--	--	--	--	0(1)	0(1)	0.00
(23°13'N, 163°09'W)	232	631	--	--	--	--	--	0(4)	0(4)	0.00
		Total	--	--	--	--	--	0(5)	0(5)	0.00
Necker Island	232	642	--	--	121(23)	--	--	--	121(23)	5.26
(23°34'N, 164°42'W)	232	643	--	168(20)	40(8)	--	--	34(4)	242(32)	7.56
	233	644	--	--	--	--	--	--	--	--
	233	645	--	39(20)	--	--	--	--	39(20)	1.95
	233	646	--	8(20)	--	--	--	--	8(20)	0.40
	234	643	--	43(20)	--	--	--	--	43(20)	2.15
	234	644	--	--	--	--	39(8)	--	39(8)	4.88
	234	645	--	--	--	--	--	--	--	--
	234	646	--	--	--	--	--	--	--	--
	235	645	--	--	72(8)	--	--	--	72(8)	9.00
	235	646	--	--	--	--	--	--	--	--
	235	647	4(12)	20(17)	--	119(27)	--	--	143(56)	2.55
	235	648	50(20)	--	--	--	--	69(12)	119(32)	3.72
	236	645	159(22)	--	--	--	1(5)	350(64)	510(91)	5.60
	236	646	74(8)	--	20(12)	512(92)	0(9)	30(6)	636(127)	5.01
	236	647	155(6)	97(16)	21(18)	33(10)	--	--	306(50)	6.12
	236	648	3(4)	--	--	99(21)	--	--	102(25)	4.08
		Total	455(72)	375(113)	274(69)	763(150)	40(22)	483(86)	2,380(512)	4.65
French Frigate	236	660	--	9(20)	--	--	0(2)	--	9(22)	0.41
Shoals	236	662	--	1(20)	--	--	--	--	1(20)	0.05
(23°46'N, 166°18'W)	236	663	--	--	--	0(11)	--	--	0(11)	0.00
	237	662	--	0(20)	--	--	--	--	0(20)	0.00
	237	663	--	--	73(35)	--	0(5)	--	73(40)	1.82
	238	662	--	--	--	--	--	2(8)	2(8)	0.25
	238	663	--	0(20)	1(10)	1(7)	--	0(8)	2(45)	0.04
	238	664	--	--	--	0(4)	--	--	0(4)	0.00
	239	662	--	--	--	--	--	0(4)	0(4)	0.00
	239	663	--	--	--	--	--	0(2)	0(2)	0.00
		Total	--	10(80)	74(45)	1(22)	0(7)	2(22)	87(176)	0.49

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Location	Grid		Fish Trap Catches						Total	Catch/ Trap Night
			1976	1977	1978	1979	1980	1981		
Brooks Banks	240	668	--	--	--	1(8)	--	--	1(8)	0.12
(24°05'N, 166°50'W)	241	667	--	--	--	--	0(2)	--	0(2)	0.00
	241	668	--	--	--	4(7)	0(3)	--	4(10)	0.40
	241	669	--	--	--	0(2)	--	--	0(2)	0.00
	242	669	--	--	--	1(4)	--	--	1(4)	0.25
		Total	--	--	--	6(21)	0(5)	--	6(26)	0.23
St. Rogatien Bank	242	670	--	--	--	1(9)	--	--	1(9)	0.11
(24°25'N, 167°15'W)	242	671	--	--	--	--	--	--	--	--
	243	670	--	--	--	--	0(3)	--	0(3)	0.00
	243	671	--	--	--	--	--	--	--	--
	244	671	--	--	--	--	--	--	--	--
		Total	--	--	--	1(9)	0(3)	--	1(12)	0.08
Bank 7 (24°36'N, 167°18'W)	246	672	--	--	--	--	0(6)	--	0(6)	0.00
Gardner Pinnacles	244	679	--	--	--	--	--	--	--	--
(25°01'N, 167°59'W)	245	680	--	--	--	--	--	0(6)	0(6)	0.00
	246	681	--	--	--	--	--	--	--	--
	247	681	--	--	0(1)	--	--	--	0(1)	0.00
	248	681	--	--	2(9)	--	--	--	2(9)	0.22
	249	682	--	--	--	--	--	5(6)	5(6)	0.83
	250	679	--	--	--	--	--	--	--	--
	250	680	--	--	--	--	--	0(1)	0(1)	0.00
	250	682	--	--	--	--	3(2)	4(4)	7(6)	1.17
	250	683	--	--	--	--	0(3)	0(2)	0(5)	0.00
	251	681	--	--	--	--	5(8)	--	5(8)	0.62
	251	682	--	--	2(9)	--	0(6)	--	2(15)	0.13
	252	680	--	--	--	1(8)	--	--	1(8)	0.12
	252	681	--	--	--	--	17(14)	--	17(14)	1.21
		Total	--	--	4(19)	1(8)	25(33)	9(19)	39(79)	0.49
Raita Bank	254	694	--	--	--	--	--	--	--	--
(25°35'N, 169°35'W)	254	696	--	4(12)	--	--	--	--	4(12)	0.33
	255	693	--	52(20)	--	--	--	--	52(20)	2.60
	255	694	--	--	5(8)	--	--	--	5(8)	0.62
	255	695	--	--	--	--	--	--	--	--
	256	693	--	--	--	--	0(2)	--	0(2)	0.00
	256	694	--	--	0(1)	--	0(2)	0(6)	0(9)	0.00
	256	695	--	--	--	--	--	--	--	--
		Total	--	56(32)	5(9)	--	0(4)	0(6)	61(51)	1.20
Maro Reef	252	704	--	137(20)	--	--	--	--	137(20)	6.85
(25°29'N, 170°35'W)	252	706	--	--	0(6)	--	--	--	0(6)	0.00
	253	704	--	33(4)	--	--	--	--	33(4)	8.25
	253	707	--	--	--	--	--	1(8)	1(8)	0.12
	253	708	--	365(60)	0(4)	--	--	--	365(64)	5.70
	254	706	--	0(4)	--	--	--	--	0(4)	0.00
	254	707	--	170(24)	27(8)	--	--	43(12)	240(44)	5.45
	254	708	--	--	0(1)	--	17(7)	32(8)	49(16)	3.06
	254	709	--	--	--	0(11)	0(6)	--	0(17)	0.00
	255	705	--	--	--	--	--	--	--	--
	255	706	--	79(24)	--	--	--	--	79(24)	3.29
	255	707	--	--	--	--	--	--	--	--
	255	708	--	--	--	75(11)	--	--	75(11)	6.82
	255	709	--	--	--	--	0(3)	--	0(3)	0.00
	256	706	--	--	--	--	1(3)	--	1(3)	0.33
	256	707	--	82(20)	--	--	--	--	82(20)	4.10
		Total	--	866(156)	27(19)	75(22)	18(19)	76(28)	1,062(244)	4.35
Northhampton Seamounts (25°18'N, 172°04'W)	254	724	--	--	--	--	0(4)	--	0(4)	0.00
Laysan Island	256	717	--	12(8)	--	--	--	--	12(8)	1.50
(25°42'N, 171°44'W)	257	716	--	34(12)	--	--	--	--	34(12)	2.83
	257	717	--	31(40)	--	--	--	--	31(40)	0.78
	257	718	--	45(14)	--	--	0(1)	--	45(15)	3.00
	258	715	--	1(4)	--	--	--	--	1(4)	0.25
	258	716	--	120(28)	--	6(20)	0(6)	--	126(54)	2.33
	258	717	--	27(12)	--	--	--	--	27(12)	2.25
	258	718	--	126(32)	--	0(11)	--	--	126(43)	2.93
		Total	--	396(150)	--	6(31)	0(7)	--	402(188)	2.14
Pioneer Bank (26°00'N, 173°25'W)	259	735	--	--	0(24)	--	--	--	0(24)	0.00

TABLE 1. CATCH OF LOBSTERS (LEGAL-SIZED, SUBLEGAL-SIZED AND BERRIED) IN LOBSTER POTS AND FISH TRAPS DURING RESEARCH AND CHARTER CRUISES TO THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976 TO SEPTEMBER 1981 (continued)

Location	Grid		Fish Trap Catches						Total	Catch/ Trap Night
			1976	1977	1978	1979	1980	1981		
Lisianski Island	258	738	--	--	--	0(8)	--	--	0(8)	0.00
(26°02'N, 174°00'W)	259	737	--	--	--	1(20)	--	--	1(20)	0.05
	259	738	--	--	--	0(3)	--	--	0(3)	0.00
	259	739	--	2(12)	--	--	--	--	2(12)	0.17
	259	741	--	2(12)	--	--	--	--	2(12)	0.17
	260	738	--	6(32)	--	--	--	--	6(32)	0.19
	260	739	--	--	--	--	--	--	--	--
	260	740	--	--	--	--	--	--	--	--
	261	739	--	0(12)	--	--	--	--	0(12)	0.00
	262	741	--	0(20)	--	--	--	--	0(20)	0.00
		Total	--	10(88)	--	1(31)	--	--	11(119)	0.09
Bank 8	262	745	--	--	0(8)	--	--	--	0(8)	0.00
(26°17'N, 174°34'W)	263	745	--	--	--	0(8)	--	--	0(8)	0.00
		Total	--	--	0(8)	0(8)	--	--	0(16)	0.00
Salmon Bank	269	763	--	--	--	--	0(5)	--	0(5)	0.00
(26°56'N, 176°28'W)	269	764	--	0(26)	--	--	--	--	0(26)	0.00
		Total	--	0(26)	--	--	0(5)	--	0(31)	0.00
Pearl and Hermes	277	757	--	0(20)	--	--	0(2)	1(5)	1(27)	0.04
Atoll	277	758	7(12)	13(12)	--	--	0(7)	0(4)	20(35)	0.57
(27°48'N, 175°51'W)	277	759	--	14(12)	--	--	0(7)	2(8)	16(27)	0.59
	277	760	--	--	--	--	--	0(13)	0(13)	0.00
	278	757	--	28(13)	--	0(11)	--	0(2)	28(26)	1.08
	278	759	--	--	--	--	--	--	--	--
	278	760	--	41(32)	--	40(34)	--	--	81(66)	1.23
	279	757	--	15(12)	--	--	--	0(6)	15(18)	0.83
	279	758	--	5(12)	--	--	--	--	5(12)	0.42
	279	759	--	--	--	4(11)	--	--	4(11)	0.36
		Total	7(12)	116(113)	--	44(56)	0(16)	3(38)	170(235)	0.72
Nero Seamount	279	779	--	--	--	--	0(6)	--	0(6)	0.00
(27°57'N, 177°58'W)										
Midway Islands	281	774	--	48(21)	--	--	--	--	48(21)	2.28
(28°12'N, 177°22'W)	282	772	--	--	--	--	--	--	--	--
	282	773	--	124(44)	62(20)	--	--	--	186(64)	2.91
	282	774	--	34(28)	62(20)	13(4)	--	--	109(52)	2.10
	283	773	--	0(4)	--	--	--	--	0(4)	0.00
	283	774	--	0(8)	--	--	--	--	0(8)	0.00
		Total	--	206(105)	124(40)	13(4)	--	--	343(149)	2.30
Kure Atoll	283	782	--	--	--	--	0(2)	--	0(2)	0.00
(28°25'N, 178°25'W)	283	783	--	7(48)	0(20)	--	--	--	7(68)	0.10
	284	782	--	2(37)	--	--	--	--	2(37)	0.05
	284	783	--	2(16)	--	--	--	--	2(16)	0.12
	285	783	--	--	--	--	0(2)	--	0(2)	0.00
		Total	--	11(101)	0(20)	--	0(4)	--	11(125)	0.09
Ladd Seamount	284	766	--	--	--	--	0(1)	0(6)	0(7)	0.00
(28°32'N, 176°40'W)	285	766	--	--	--	--	0(6)	0(16)	0(22)	0.00
		Total	--	--	--	--	0(7)	0(22)	0(29)	0.00
Bank 11	288	795	--	--	--	--	0(1)	--	0(1)	0.00
(28°53'N, 179°38'W)	289	795	--	--	--	--	0(4)	--	0(4)	0.00
		Total	--	--	--	--	0(5)	--	0(5)	0.00
SE Hancock Seamount	298	790	--	--	0(4)	--	0(5)	--	0(9)	0.00
(29°47'N, 179°04'E)										
NW Hancock Seamount	302	787	--	--	0(4)	0(1)	--	--	0(5)	0.00
(30°16'N, 178°43'W)										

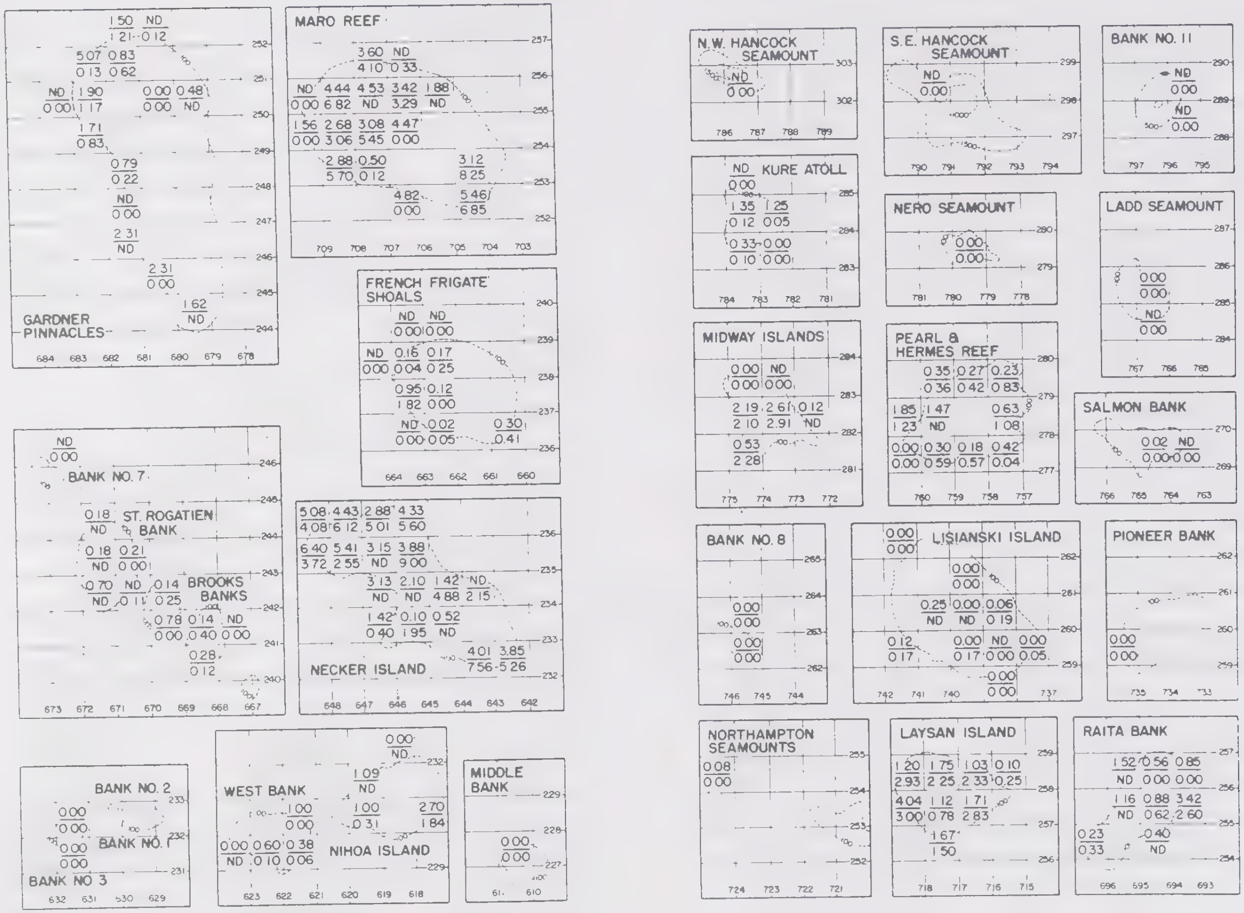
GARDNER PINNACLES
MARO REEF
FRENCH FRIGATE SHOALS
BANK NO. 7
ST. ROGATIEN BANK
BROOKS BANKS
NECKER ISLAND
BANK NO. 2
BANK NO. 1
BANK NO 3
WEST BANK
NIHOA ISLAND
MIDDLE BANK
N.W. HANCOCK SEAMOUNT
S.E. HANCOCK SEAMOUNT
BANK NO. 11
KURE ATOLL
NERO SEAMOUNT
LADD SEAMOUNT
MIDWAY ISLANDS
PEARL & HERMES REEF
SALMON BANK
BANK NO. 8
LISIANSKI ISLAND
PIONEER BANK
NORTHAMPTON SEAMOUNTS
LAYSAN ISLAND
RAITA BANK
ND

Figure 3. Distribution of spiny lobster catch rates by lobster traps (upper figure) and fish traps (lower figure) for 0.1° squares in the Northwestern Hawaiian Islands, October 1976 to September 1981. (ND = No data)

P. marginatus was also found around the islands and atolls farther up the chain. At Maro Reef, which contrasted sharply with Necker in substratum condition, high catch rates of *P. marginatus* were also obtained. The surveys conducted at Maro Reef in 1977 produced catch rates varying between 2.88 and 6.19 individuals/pot-night, whereas the fish traps produced catches ranging from 0.00 to 8.25 individuals/pot-night. The high abundance at Maro Reef was unexpected because subsurface observations made during a cruise in 1977 revealed a substratum of predominantly sand and sandstone just outside that coral reef; however, subsequent discussions with other investigators who dove at Maro Reef brought out the fact that many areas in the 10 to 55 m depth range have suitable lobster habitat. Due to the high catch rates, Maro Reef was established as the second important area in the spiny lobster fishery.

Beyond Maro Reef, none of the sites surveyed showed commercial concentrations of *P. marginatus*, although several had moderately good catch rates. Whether a commercial fishery can be developed at these sites depends to a large extent on the cost of operating at such distances from the home port. Few lobsters were found at Northampton Seamounts, but relatively good catches were made at several sites (grids 257716, 257718, 258716, 258717, 258718) at Laysan Island. Pioneer Bank near Lisianski Island produced nothing and catches at Lisianski, which has a rather large bank, were extremely low at all the sites surveyed.

Bank 8 and Salmon Bank received very little effort; the former produced nothing and only two lobsters were caught in 87 pot-nights and 31 trap-nights at the latter. At Pearl and Hermes Atoll, the entire area outside the reef was surveyed and good catches were made along the central western edge of the bank (grids 278759 and 278760); other survey sites produced relatively small catches.

At Nero Seamounts, 24 pot-nights and 6 trap-nights of effort produced no spiny lobsters, but at Midway Islands, the catch rates were over 2 individuals/pot-night and trap-night in three grids (281774, 282773, and 282774). At the extreme northwestern end of the Hawaiian Archipelago, *P. marginatus* was found at Kure Atoll but not in the same numbers as at Midway. Kure marks the northern limit of the distribution of *P. marginatus* as none were found at Ladd Seamount, which is located slightly north of Kure, nor at Bank 11 and Hancock Seamounts to the northwest.

Simpson (1976) speculated that for *P. argus*, areas which are conducive to high survival could be associated with bottom topography, that is, there are many suitable hiding places for the young stages to molt safely. This is believed to be a plausible explanation for the high densities of spiny lobster at Necker and Maro Reef.

Catch by Depth

Although P. marginatus has been reported at depths ranging from 110 to 183 m in Hawaiian waters (McGinnis, 1972), we believe the species is not found at depths beyond 137 m[1]. The surveys indicated that this species was usually found in water depths of 90 m or less. The relative abundance of spiny lobster taken in lobster pots and fish traps by 9-m strata was calculated for each of the islands and banks (Figure 4). Along the lower portion of the archipelago the relative abundance was highest at the 55 to 64 m depth around Nihoa and Necker and at the 65 to 73 m depth around French Frigate Shoals. Farther northward at Gardner Pinnacles, the relative abundance of spiny lobsters was higher at shallower depths of 19 to 27 m to about 46 to 54 m.

At Raita Bank, the relative abundance was highest between 28 and 36 m. Northwestward at Maro Reef, there was a dramatic shift in relative abundance: the highest values were in the shallowest area. This trend towards higher abundance at shallower depth appeared to be consistent at the remaining islands, banks, and atolls to the northwest of Maro Reef. Uchida et al. (1980b) suggest that the relatively low catch rates observed in waters deeper than 64 m in the northern part of the archipelago may be the result of differences in the temperature regime from north to south in the NWHI.

The proportion of legal-sized, sublegal-sized, and berried female lobsters were also examined by depth for Necker and Maro Reef, because of the importance of these areas for commercial trapping (Figure 5). At Necker, it was found that catches at the 19 to 27 m depth were composed predominantly of sublegal-sized lobsters, but at the 28 to 36 m depth the proportion of legal-sized and sublegal-sized lobsters was nearly 1:1. At depths deeper than 36 m, however, legal sizes predominated by a slight margin. At Maro Reef, legal-sized lobsters predominated at the shallowest depth by a small margin. At the 10 to 18 m depth sublegal-sized lobsters were predominant, comprising 60 percent of the catch. The catches at depths greater than 18 m were composed of legal-sized lobsters by a very wide margin over sublegal-sized lobsters.

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[1] McGinnis (1972) cited cruise report 35 of the Townsend Cromwell, prepared by the Bureau of Commercial Fisheries (now NMFS), and which involved shrimp, Penaeus marginatus, trawling operations. McGinnis assumed that the by-catch of spiny lobster, Panulirus marginatus, was also made at the same depths trawled for shrimp. The original catch records reveal that 22 spiny lobsters were captured on the bank north of Molokai between Kaiehu Point and Paualaia Point during four trawl hauls on April 6, 1968 in waters which averaged 110, 124, 128, and 137 m in depth.

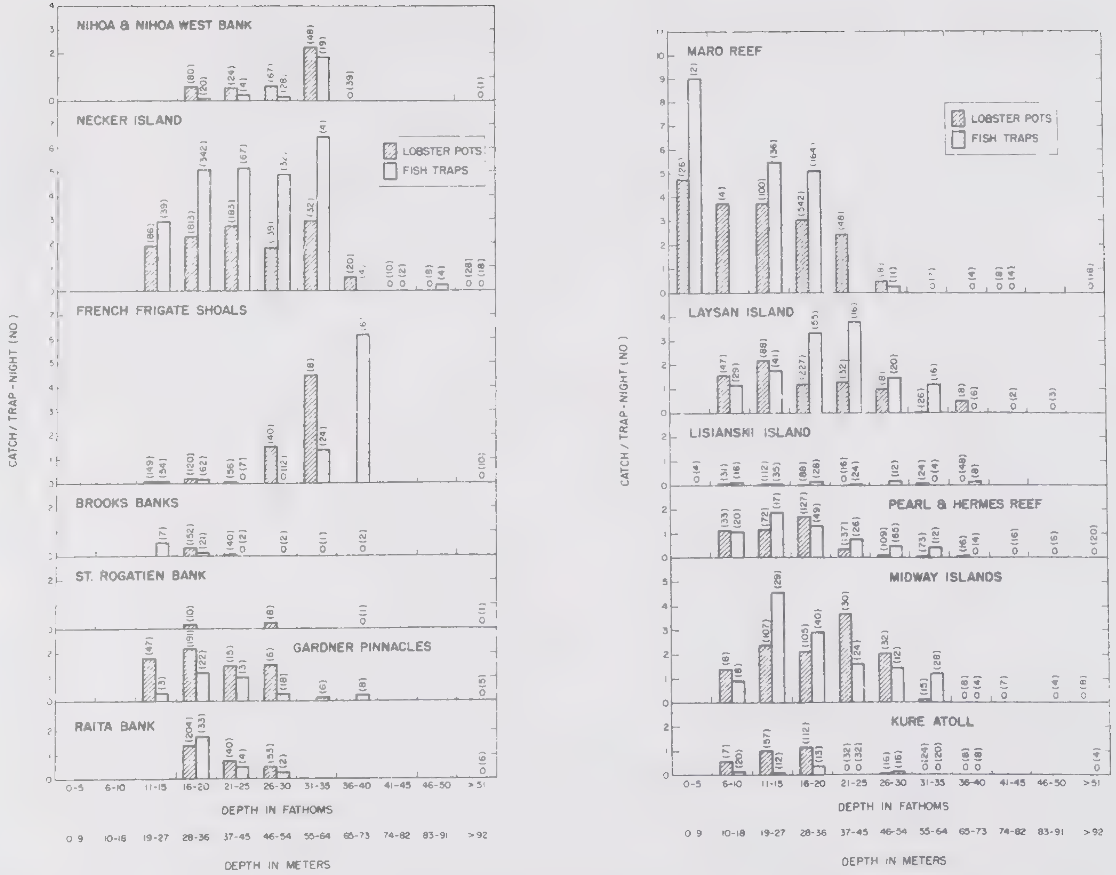

Figure 4. Distribution of spiny lobster catch rates, by depth, in the Northwestern Hawaiian Islands, October 1976 to September 1981. (No.) = effort in pot-night or trap-night

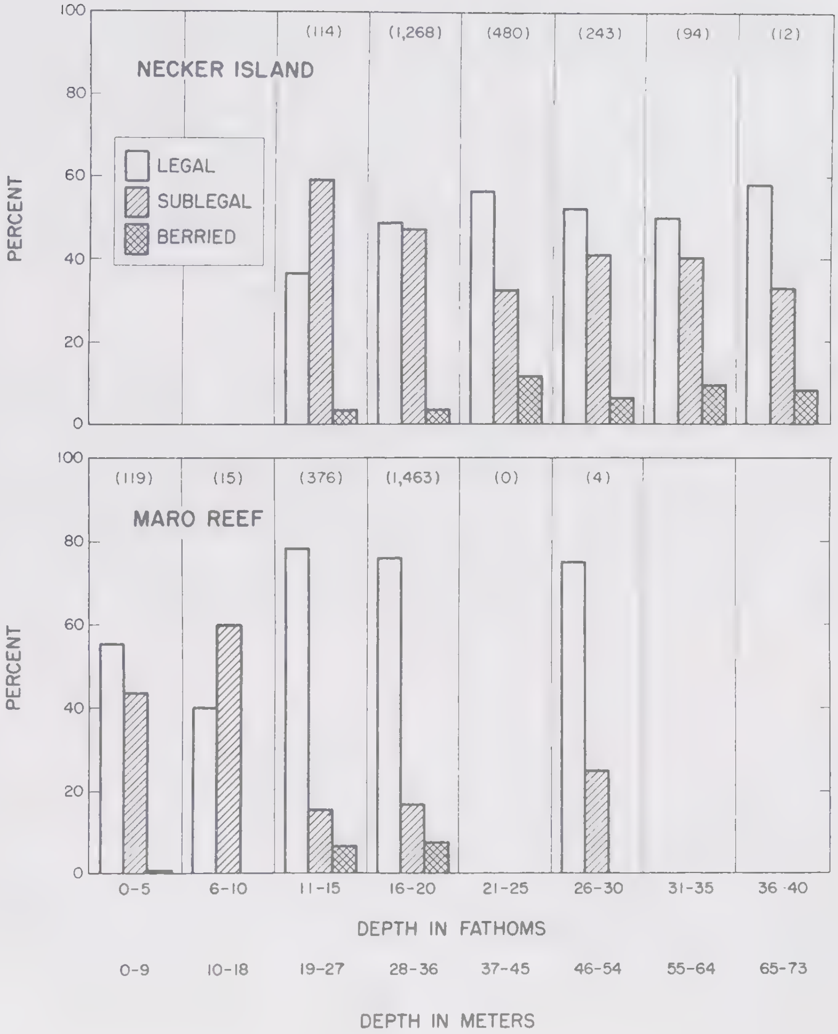

Figure 5. Percentage of legal, sublegal, and berried (ovigerous) female lobsters in catches by depth at Necker Island and Maro Reef, October 1976 to September 1981. (No.) = number of lobsters; zero indicates effort expended at that depth range but no lobsters caught.

Life History

To satisfy the data needs of the Western Pacific Regional Fishery Management Council, and also to fill gaps in the knowledge of the life history of _P. marginatus_ in the NWHI, studies on several aspects of the life history, including fecundity and spawning (Honda, 1980, in preparation), growth and movement (Uchiyama, in preparation), size at maturity (Prescott, in preparation), behavior (reaction to offal) (Gooding, in preparation), and predators (Gooding, 1979, 1982), of _P. marginatus_ were conducted. The results of these studies are reviewed in the following sections.

FECUNDITY AND SPAWNING

Fecundity of _P. marginatus_ from Oahu was estimated by Morris (1968) and McGinnis (1972). Fecundity studies conducted by Honda (1980, in preparation) on NWHI _P. marginatus_ collected between 1978 and 1981 are based on egg counts of 75 samples of egg masses from berried females at Necker and Maro Reef. The slopes of the regression of fecundity on CL for the Maro Reef and Necker samples were not significantly different. Honda also showed that fecundity increased with size. The fecundity-CL relationship (Maro Reef and Necker samples pooled) is described by the equation:

$$Y = 6.5334CL^{2.3706}$$

where

CL = carapace length in millimeters, and
Y = number of eggs carried

When compared with fecundity estimates for Oahu, Honda found that the NWHI estimates were in rather close agreement as far as the smaller females were concerned; however, the discrepancy between Oahu and NWHI estimates became greater for the larger females. For example, at 110-mm CL, an NWHI female was estimated to carry 460,000 eggs whereas an Oahu female had an estimated 575,000 eggs.

The percentage of berried females in the catch was examined by month at Necker and Maro Reef (Table 2). Using only data for reproductively mature females of 60.7-mm CL (see section on "Size at Maturity" below) it was found that between 9 and 23 percent of the female population at Necker was berried in all months of the year except January (no data available) and August, when only 19 male and 5 non-berried female lobsters were captured. Data on berried females from Maro Reef were even sparser; however, it appears evident that spawning occurs at least during the summer. Data for other months are either not available or too sparse to be meaningful.

TABLE 2. PERCENTAGE OF BERRIED FEMALE IN THE CATCH AT NECKER ISLAND AND MARO REEF, BY MONTH, BASED ON DATA COLLECTED DURING FISH AND LOBSTER TRAPPING OPERATIONS, OCTOBER 1976 TO SEPTEMBER 1981

	Necker Island			Maro Reef		
	Total Female	Berried		Total Female	Berried	
		Total	%		Total	%
January	--	--	--	--	--	--
February	44	8	18	--	--	--
March	98	9	9	--	--	--
April	65	12	18	60	10	17
May	254	51	20	165	31	19
June	163	24	15	577	103	18
July	215	42	20	266	51	19
August	5	0	0	39	10	26
September	350	80	23	--	--	--
October	185	34	18	362	23	6
November	191	20	10	--	--	--
December	22	5	23	8	2	25

Of 8,304 females caught on research and charter cruises to the NWHI, information on the presence or absence of the sperm packet or spermatophores was recorded for about a third or 2,716 individuals. The smallest mated female measured 48.3-mm CL and the largest 140.0-mm CL. The percentage of mated females was highest among those between 80.00 and 89.0-mm CL. Of 774 mated sublegal-sized (<77.0-mm CL) females collected during the surveys, 673 individuals or 87 percent were from Necker, indicating that copulation takes place in greater numbers there among sublegal-sized females than at any other site in the NWHI.

Of the 668 berried females measured, nearly 63 percent were between 80.0 and 99.0-mm CL. The smallest berried female, caught at Necker, measured 49.5-mm CL whereas the largest, from Maro Reef, was 132.5-mm CL. The Necker population of females apparently spawned at a smaller size; of 165 berried sublegal-sized females sampled throughout the NWHI, 137 individuals or 83 percent were from Necker.

GROWTH AND MOVEMENT

Lobsters were tagged to collect data on growth, movement, and abundance. Of 5,367 lobsters tagged during the early phases of the investigation, 139 were recaptured, either by commercial vessels or on research cruises. Tagged lobsters ranged from 45.3

to 145.8-mm CL; recaptures were from 68.0 to 100.3-mm CL. Considerable difficulty was experienced with tags; many of the vinyl and polyurethane tags, when recovered, were worn down to small stubs as if chewed on by other lobsters. Also 98 or 70 percent of the recoveries either were not accompanied by any CL measurements or showed no positive growth which would be useful for determing growth rates. As a result, analysis was restricted to modes in the length-frequency data collected from the northern sector of Necker Island on four cruises during 1976-78. Confining the analysis to data from the northern sector of Necker bank reduced variability attributable to differences in habitat, stock density, stages of exploitation, and population structure.

Whereas a progression of modes was evident in the male length-frequency distribution, that for the females was unimodal and the mode appeared to regress with time (Uchiyama, in preparation). Including the lobster puerulus, a von Bertalanffy growth curve was constructed based on modal progression in the length-frequency distribution of males collected at Necker Island (Figure 6).

Based on tagging data published by McGinnis (1972) the growth of male and female lobsters caught around Oahu were estimated and compared with the male growth curve from Necker. The curves are similar for the males. Data on growth rates furnished by C. MacDonald (1983: personal communication) indicated that lobsters at Kure Atoll and French Frigate Shoals grows slightly faster than those around Necker and Oahu.

Although the tag recovery data were not appropriate for calculating the growth curve, sufficient data was obtained on recapture location to determine the movement of lobsters. For tagged lobsters which were recovered by a NMFS research vessel, or by commercial vessels carrying NMFS observers, the recapture locations were determined rather precisely; however, for those recoveries made by commercial vessels with no NMFS observer aboard, reliance was made on data supplied by the captain. Of 94 recoveries with usable data, 85 (90 percent) showed movement of 5 nmi or less. Only 9 (10 percent) had traveled more than 5 nmi, the farthest being 15.6 nmi. No correlation was found between CL and distance traveled ($r = -0.102$; d.f. = 92; $P > 0.05$) or between days at liberty and distance traveled ($r = 0.226$; d.f. = 92; $P > 0.05$). Twenty-one lobsters (22 percent) were at liberty for 30 days or less, 49 (53 percent) for 31 to 60 days, and 11 (12 percent) for 61 to 90 days. The remaining 13 (14 percent) were at liberty for 322 days.

SIZE AT MATURITY

Most of the past studies on size at maturity have been based on females because males lack satisfactory indicators of sexual maturity. Studies by Heydorn (1965, 1969), Berry (1973), and Aiken and Waddy (1980) on size at maturity of male lobsters are

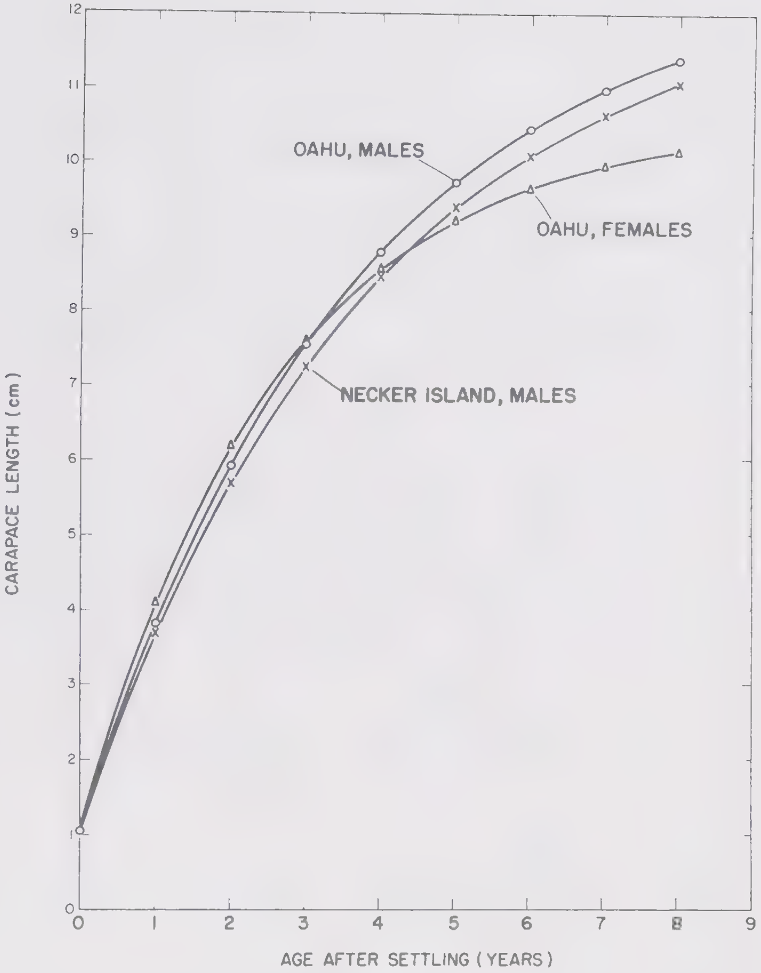

Figure 6. Growth curve of spiny lobsters from Necker Island and Oahu

Oahu male: L = 12.77 cm; K = 0.2698
Oahu female: L = 10.60 cm; K = 0.3857
Necker male: L = 12.46 cm; K = 0.2632

based on either weight or stage of development of the vas deferentia.

Among the secondary sexual characteristics in male spiny and clawed lobsters, length of the walking legs was found to increase significantly in some species as the lobster grew. George and Morgan (1979) for *P. versicolor* and Grey (1979) for *P. cygnus* estimated the size at maturity using linear growth phases of the walking legs.

Estimates of the size at maturity of *P. marginatus* were obtained from populations around Oahu and Necker Island (Prescott, in preparation). Using regression analysis, Prescott estimated size at maturity from changes in the allometric growth of pairs of walking legs. For the Oahu population, Prescott found that males mature at 63.6-mm CL and females at 58.6-mm CL, a difference in CL of 5.0 mm. For the Necker Island population, Prescott obtained estimates of 59.2-mm CL for males and 60.7-mm CL for females. No significant differences were found in size at maturity between sexes and between localities. The size at maturity estimated for Necker females is considerably larger than the size of the smallest mated female found there (48.3-mm CL); however, this discrepancy does not invalidate Prescott's results because the presence of spermatophores is not conclusive evidence that the female has mature ovaries (Wilson, 1948).

Population Structure

SIZE COMPOSITION

The percentage frequency distributions of carapace lengths of male and female spiny lobsters caught during our surveys are given by island and bank in Figure 7. Because there are wide temporal and spatial gaps in sampling, only a descriptive summary of size differences among areas and between sexes is provided.

It was shown earlier that the size of lobsters differed with locality (Uchida et al., 1980a). Because catches from both fish traps and lobster pots are included in the samples from almost all of the localities surveyed, differences in size reflect the population and not an artifact of the sampling gear.

Moving from Nihoa northwestward, the lobsters were smallest at Necker and only slightly larger at French Frigate Shoals. At these localities, the average size was much smaller than that from other islands and banks, even during earlier surveys (Uchida et al., 1980a). Therefore, the small sizes, particularly at Necker, do not represent a gradual reduction in size caused by increasing fishing effort and removal of the large adults. Farther north, no apparent trend or cline in the average size of the lobsters was found; the largest lobsters were found at Kure Atoll where the males averaged 116-mm CL followed by those at Brooks Banks where the males averaged 113-mm CL (Table 3).

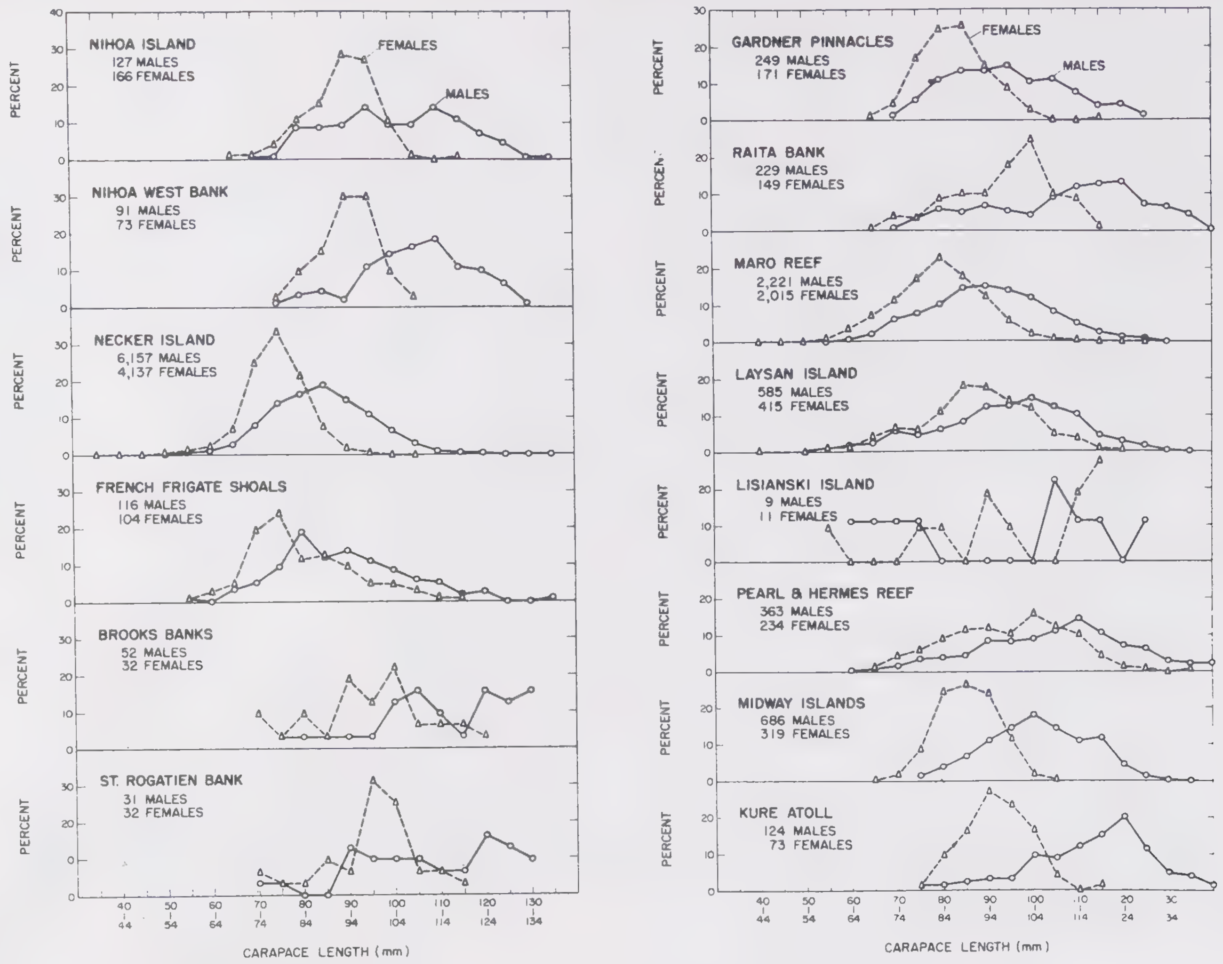

Figure 7. Percentage frequency distribution of carapace lengths of male and female spiny lobsters sampled in the Northwestern Hawaiian Islands, October 1976 to September 1981

TABLE 3. THE SIZE RANGE, MEAN CARAPACE LENGTH, STANDARD DEVIATION, AND VARIANCE OF MALE AND FEMALE SPINY LOBSTERS SAMPLED IN THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976 TO SEPTEMBER 1981

Location	Male				Female			
	Size Range (cm)	Mean Carapace Length (cm)	Standard Deviation	Variance	Size Range (cm)	Mean Carapace Length (cm)	Standard Deviation	Variance
Nihoa	7.18 to 13.56	10.41	1.3964	1.9499	6.72 to 11.70	9.21	0.7513	0.5644
Nihoa West Bank	7.66 to 13.15	10.86	1.1677	1.3636	7.60 to 10.61	9.30	0.6317	0.3990
Necker Island	4.28 to 13.70	8.70	1.0895	1.1869	3.37 to 10.52	7.71	0.6739	0.4542
French Frigate Shoals	5.96 to 13.51	9.16	1.3793	1.9024	5.62 to 11.56	8.25	1.1577	1.3402
Brooks Banks	7.59 to 13.50	11.31	1.5870	2.5186	7.36 to 12.01	9.70	1.3102	1.7165
St. Rogatien Bank	7.25 to 13.18	11.06	1.6002	2.5606	7.39 to 11.94	9.73	1.0290	1.0589
Gardner Pinnacles	7.21 to 12.79	9.75	1.2862	1.6543	6.77 to 11.70	8.58	0.7559	0.5713
Raita Bank	7.49 to 14.31	11.06	1.6722	2.7963	6.98 to 11.70	9.67	1.0685	1.1417
Maro Reef	4.74 to 13.67	9.34	1.3190	1.7397	4.38 to 13.25	8.70	0.9906	0.9813
Laysan Island	5.19 to 13.90	9.69	1.5332	2.3508	4.48 to 12.40	9.01	1.2588	1.5847
Lisianski Island	6.15 to 12.94	9.50	2.4550	6.0268	6.00 to 11.88	9.82	1.9997	3.9990
Pearl and Hermes Atoll	6.05 to 14.91	10.84	1.7121	2.9312	6.77 to 14.00	9.74	1.3509	1.8249
Salmon Bank	7.72 to 12.51	10.90	2.7569	7.6004	8.54 to 11.25	9.90	1.9162	3.6720
Midway Islands	7.53 to 13.64	10.34	1.1122	1.2369	6.73 to 10.94	8.78	0.6539	0.4275
Kure Atoll	7.71 to 14.34	11.55	1.3510	1.8253	7.91 to 11.85	9.45	0.7227	0.5223

There is no known explanation for the small size of lobsters at Necker. It has been speculated that there may be a density-dependent effect on growth rate caused by intraspecific competition (Uchida et al., 1980a). Such an effect could occur in a large population over a limited area and may account for the high catch rates at Necker. Also, if most of the food energy available to lobsters at Necker was converted into egg production, then one would expect not only small sizes associated with impaired somatic growth, but also a smaller size at maturity. Data presented earlier on percentage of ovigerous and mated females at Necker provide evidence supporting this conclusion. Chittleborough (1979) also reported that when the density of the breeding stock is high, the mean size at maturity is low and the adults are generally stunted.

The size of the sexes also differed. In every area except Lisianski, where the sample size was too small to be meaningful, males were consistently predominant among the large size classes. The differences in average size between sexes is thought to result from dimorphism related to egg bearing in females (Heydorn, 1969). Simpson (1976) cited a faster growth rate or reduced mortality among males, or both, in accounting for the predominance of males in populations of *P. argus*. MacDonald (in Prescott, in preparation) believes that growth rate per se does not account for the difference in size between the sexes for *P. marginatus*. Rather it is reduced mortality among males that is responsible for their predominance in the population.

RATIO OF LEGAL-SIZED TO SUBLEGAL-SIZED LOBSTERS

The lobster catches based on a legal size of 82.5-mm CL were analyzed in an earlier study (Uchida et al., 1980a). However, because of a new legal minimum size of 77.0-mm CL for the NWHI lobster, the ratio between legal and sublegal sizes was calculated (Table 4). Apparently, the ratios have not changed drastically from those calculated earlier.

The ratio of legal- to sublegal-sized lobster, by locality, for pot catches during October 1976 to September 1981 varied widely between 51:49 at Necker and 97:3 at Kure. For fish trap catches, where the number of sublegal-sized lobsters would be expected to be higher, the ratios varied from 39:61 at Necker to 100:0 at several banks; however, if those banks where less than 25 lobsters were taken by fish traps are not counted, then the ratio is closer to 94:6.

Except at Necker and French Frigate Shoals where the catch of sublegal-sized lobsters was as high as if not higher than legal lobsters, the proportion of sublegal-sized lobsters in the NWHI is expected to be low, because juveniles molt more frequently than adults, tend to remain secluded and, hence, are not subject to capture. They are, however, more susceptible to

TABLE 4. THE LEGAL TO SUBLEGAL SIZE RATIO AND MALE TO FEMALE SEX RATIO OF CATCHES BY LOBSTER POTS AND FISH TRAPS DURING RESEARCH CHARTER CRUISES IN THE NORTHWESTERN HAWAIIAN ISLANDS, OCTOBER 1976 TO SEPTEMBER 1981

Island/Bank	Gear	Legal Size			Male: Female Sex Ratio	Sublegal Size			Male: Female Sex Ratio	Total Male	Total Female	Male: Female Sex Ratio	Legal: Sublegal Size Ratio
		Male No.	Female No.[1]	Total No.		Male No.	Female No.[1]	Total No.					
Nihoa	Lobster	110	83	193	57:43	5	9	14	36:64	115	151	43:57	93:7
	Fish	16	12	28	57:43	3	1	4	75:25	19	21	48:52	88:12
Nihoa West Bank	Lobster	80	44	124	64:36	3	2	5	60:40	83	64	56:44	96:4
	Fish	2	1	3	67:33	0	0	0	0:0	2	1	67:33	100:0
Necker Island	Lobster	3,343	516	3,859	87:13	1,531	2,110	3,641	42:58	4,874	3,307	60:40	51:49
	Fish	649	114	763	85:15	611	594	1,205	51:49	1,260	860	59:41	39:61
French Frigate Shoals	Lobster	56	30	86	65:35	20	32	52	38:62	76	64	54:46	62:38
	Fish	26	13	39	67:33	14	24	38	37:63	40	41	49:51	51:49
Gardner Pinnacles	Lobster	298	144	442	67:33	27	53	80	34:66	325	236	58:42	85:15
	Fish	20	6	26	77:23	4	5	9	44:56	24	11	68:32	76:26
Brooks Banks	Lobster	26	22	48	54:46	1	1	2	50:50	27	30	47:53	96.4
	Fish	5	2	7	71:29	0	0	0	0:0	5	2	71:29	100:0
St. Rogatien Bank	Lobster	30	26	56	54:46	1	3	4	25:75	31	32	49:51	93:7
	Fish	—	—	—	—	—	—	—	—	—	—	—	--
Raita Bank	Lobster	419	258	677	62:38	18	24	42	43:57	437	290	60:40	94:6
	Fish	35	20	55	64:36	2	4	6	33:67	37	24	61:39	90:10
Maro Reef	Lobster	1,405	980	2,385	59:41	313	331	644	49:51	1,718	1,626	51:49	79:21
	Fish	417	246	663	63:37	147	149	296	50:50	564	481	54:46	69:31
Laysan Island	Lobster	306	195	501	61:39	33	32	65	51:49	339	249	58:42	89:11
	Fish	177	92	269	66:34	66	61	127	52:48	243	168	59:41	68:32
Lisianski Island	Lobster	2	5	7	29:71	2	0	2	100:0	4	5	44:56	78:22
	Fish	3	1	4	75:25	2	3	5	40:60	5	6	45:55	44:56
Pearl and Hermes Atoll	Lobster	229	137	366	62:38	11	11	22	50:50	240	161	60:40	94:6
	Fish	92	61	153	60:40	4	5	9	44:56	96	72	57:43	94:6
Midway Islands	Lobster	440	156	596	74:26	17	34	51	33:67	457	215	68:32	92:8
	Fish	222	82	304	73:27	8	25	33	24:76	230	113	67:33	90:10
Kure Atoll	Lobster	117	60	177	66:34	2	4	6	33:67	119	69	63:37	97:3
	Fish	6	3	9	67:33	0	0	0	0:0	6	5	55:45	100.0

[1] Excludes berried females
Includes berried females

predation because of their smaller size. Furthermore, the initial catches at any given locality would tend to include a large proportion of the large older individuals, particularly males, partly because of their aggressive behavior. This display of dominance for shelter and food exists in a natural environment (Chittleborough, 1974). In a fishery, however it is the baited trap that becomes an object of dominant behavior.

That large lobsters were removed from the population early in the fishery was quite evident from changes in the proportion of legal lobsters in the catches at Necker. In November 1976 when trapping operations first began, the ratio of legal- to sublegal-sized lobsters at grid 236646, located north of Necker Island, was 60:40 but dropped to 43:57 by May 1977 and declined to 34:66 by August 1977. The rapid decline in the proportion of legal-sized lobsters is attributable to heavy fishing pressure by the commercial vessels.

SEX RATIO

The study data show that for lobsters taken in the NWHI, some selectivity was evident in that the proportion of females was usually lower among the legal sizes whereas it was higher among sublegal sizes in most areas sampled. Among the areas sampled, several had small sample sizes and it is believed that the ratios calculated are unlikely to be representative of the populations at those locales. For this analysis, samples with less than 10 lobsters were ignored. For the lobster pot catches, the male and female ratio among legal-sized lobsters varied from 87:13 at Necker to 54:46 at Brooks Banks and St. Rogatien Bank. For fish trap catches, the ratios were not dissimilar, ranging from 85:15 at Necker to 57:43 at Nihoa.

Among sublegal-sized lobsters, the male to female ratio was near 50:50 at Maro Reef, Laysan, and Pearl and Hermes Atoll but considerably in favor of the females at Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Raita Bank, Midway, and Kure. The fish trap catches reflect a somewhat similar preponderance of females. Whereas it was near 50:50 or very slightly in favor of males at Necker, Maro Reef, and Laysan, the ratios were largely in favor of females at French Frigate Shoals and Midway. Samples from other areas were too small to be representative. Therefore, although male predominance in the catch is evident at almost every bank among legal-sized lobsters, it is not reflected in the catch of sublegal-sized lobsters.

MORPHOMETRIC STUDIES

A study of the relationship between CL and total weight was completed in 1979 (Uchida et al., 1980a). Six hundred five lobster measurements and weights collected from Necker, Maro Reef, and French Frigate Shoals were used. Because there is sexual dimorphism in the growth of spiny lobsters, the exponential model, $W = aCL^b$, was fitted to data for males and females by the least squares method after log transformation. The length-weight relationships for the 408 males and 197 females are:

$$\text{Males:}\quad W = 0.00423CL$$

$$\text{Females:}\quad W = 0.00090CL$$

where

W = weight (g), and
CL = carapace length (mm).

The relationships are shown in Figure 8. For lobsters having a CL of 77.0 mm, the equations predict a total weight of 378.1 g (13.3 oz) for males and 402.4 g (14.2 oz) for females.

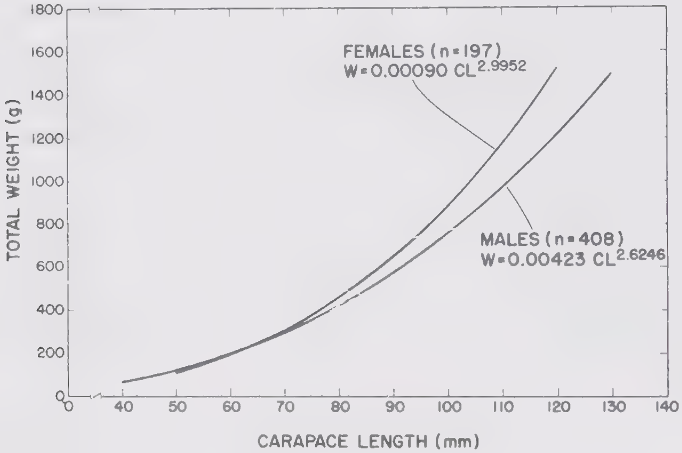

Figure 8. Length-weight relationship of male and female Panulirus marginatus determined from samples collected at Necker Island, French Frigate Shoals, and Maro Reef

For enforcement purposes in situations where a vessel lands only frozen tails, it is useful to know the relationship between tail weight or tail width, provided that either one is used as a criterion for minimum legal size. Uchida et al., (1980a) fitted exponential models to data for male and female CL and frozen tail weight and obtained:

$$\text{Males:}\quad TW = 0.00731CL$$

$$\text{Females:}\quad TW = 0.00094CL$$

where

TW = tail weight (g), and
CL = carapace length (mm).

The equations predict that lobsters with a CL of 77.0 mm would have a tail weight of 130.4 g (4.6 oz) for males and 156.3 g (5.5 oz) for females.

To determine whether a lobster was of legal size when captured, based on frozen tail width, a discriminant analysis procedure to classify them was performed (Polovina and Tagami, 1981). Based on the discriminant analysis, a lobster in which the width of the first tail segment equals or exceeds 49 mm can be classified as legal size.[2] The discriminant analysis correctly classified 94.8 percent of the sublegal-sized and 85.8 percent of the legal-sized lobsters. The tolerance factor adopted was that no more than 15 percent of the total number of tails may be less than the specified tail width limit.

MAXIMUM SUSTAINABLE YIELD (MSY)

In the NWHI, the fishery for spiny lobster is based on a single homogeneous stock within the archipelago (Shaklee and Samollow, 1980). A model developed to assess the fishery for _P. marginatus_ therefore addressed the Hawaiian population as a single stock (Polovina and Tagami, 1980).

Polovina and Tagami assumed that the ratio of natural mortality to recruitment was constant and used changes in catch/pot-night at Necker during November 1976 to April 1979 to make the first preliminary assessment of the fishery. Because the fishery was relatively new and historical catch data were not available, they used data from research cruises as well as available commercial data to estimate population size and catchability. They derived an estimate of the initial population size of 132,400 legal-sized lobsters (≥82.5-mm CL) in Region I, which is the northern, most heavily fished sector of Necker bank. By April 1979, according to their analysis, this population was reduced to 68,571 legal-sized lobsters. Their study concludes that Region I had a sustainable yield of 10,000 to 21,000 legal-sized lobsters which translated to a density estimate of 13.3 to 27.5 legal-sized lobsters/km^2/year.

Considering the possibility that the legal minimum size could be lowered, Polovina and Tagami used a Beverton-Holt equilibrium yield model to estimate yield per recruit at several levels of fishing intensity and minimum CL. They determined that a minimum legal size of 67.5 mm would produce the maximum yield per recruit. A worst-case situation would result in a decrease of 15 percent in yield per recruit at a minimum legal size of 67.5 mm as compared with a 82.5-mm minimum legal size. In the best case, a 167 percent increase in yield per recruit would result. This analysis, however does not consider the effects that a lowered minimum legal size would have on stock reproductive potential.

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[2] The spiny lobster Fishery Management Plan was approved with a 50-mm requirement.

Extrapolating the region I estimates to the entire population in the NWHI provided possible MSY ranges of 210,000 to 435,000 lobsters/year. Adjusting for differences in the geographic distribution of lobsters within the NWHI and using catch rates obtained during research cruise surveys, Polovina and Tagami also calculated lower ranges of possible MSY values of 200,000 to 378,000 lobsters/year. They also determined that although the precise magnitude of the impact of lowering the legal minimum size cannot be determined conclusively, it appears that a 15 percent increase in yield would be sustainable if the minimum legal size were reduced to 77.0 mm.

The Western Pacific Regional Fishery Management Council has adopted a range of MSY of 200,000 to 435,000 lobsters/year in the NWHI. These estimates were based on a minimum legal size of 82.5 mm, but the yield per recruit analysis suggests that a higher yield is possible at the new minimum legal size of 77.0 mm. The estimates, therefore, are on the conservative side. The accumulation of commercial data will permit future analysis to derive more precise estimates.

Exploitation

GEAR COMPETITION EXPERIMENTS

It may be argued that a decline in catch per pot-night of spiny lobsters may not represent an actual decrease in numbers but may reflect instead the results of competition among the pots for the same lobster. If spacing distances are small, the capturing fields overlap, thus resulting in an apparent decline in catch per pot-night.

Studies conducted in 1977 during research and charter cruises showed that gear competition does exist and that it is density dependent (Polovina, 1980). The highest catch rates were obtained with pot spacing in the range of 35 to 46 m (20 to 25 fathoms). From experiments conducted on the NMFS research vessel, where five spaces of 18, 27, 36, 46, and 55 m (10, 15, 20, 25, and 30 fathoms) per location were tested, spacing effects were significant for medium density areas but not in low-density and high-density areas. For data obtained from a chartered commercial vessel, no significant differences in catch rates between 36 and 55-m (20 and 30 fathoms) spacings at either high-density or very high-density areas were found. Furthermore, the catch rate with pot spacing of 18 m (10 fathoms) was significantly lower than catch rates obtained with 36 and 55-m (20 and 30 fathoms) spacing.

ESCAPE GAP AND GHOST FISHING EXPERIMENTS

In a study to determine whether the use of escape panels or vents would significantly reduce the number of sublegal sizes taken by pots, tank experiments were conducted using different-sized escape gap widths (Paul, in preparation). She found that the overall escape rate of sublegal-sized lobsters was about 60 percent and that escape rate decreased linearly with an increase in CL. No significant differences were found in escape rates of males and females. There were, however, notable differences in escape rate depending on the types of vents used and Paul concluded that vent effectiveness depends more on total vent area than on width of the vent.

In all trials conducted, it was found that unbaited traps in which live lobsters were present attracted other lobsters or ghost fished. To examine the degree of ghost fishing in lost traps, several field trials were conducted. Although lobsters are attracted to and enter unbaited pots that contained live lobsters, there was also evidence that lobsters can easily escape through the pot entrance over a period of up to 1 week. There was also evidence of cannibalism and molting among trapped lobsters.

Longer-term tests over periods of 3 weeks to 1 month indicated that lost pots can and do attract lobsters. In one test, it was observed that of 38 live, marked lobsters left in unbaited traps, 22 individuals or 58 percent remained in the same pots after 4 days. One individual left one pot and entered another. The pots also captured 14 new, unmarked lobsters. The new entries were marked and left with the remaining 22 marked lobsters and the pots were reset. At the end of the experiment, 26 days after it began, only one marked lobster remained together with five new entries, three of which were dead. All other lobsters were missing and presumed to have escaped through the entrance. These results contrast with those of Paul who found ghost fishing to be a big problem; the study data indicate that although ghost fishing does occur, there is also a high escape rate over the long term.

REACTION TO OFFAL

It became apparent soon after the Hawaiian fishery began that the vessels would begin landing a large proportion of the catch as frozen tails for the export market. A question arose of whether the offal (heads) of tailed lobsters discarded on the trapping grounds would affect the distribution and catch rates of lobsters. Declines in catch rates caused by lobster offal have been documented, and discarding offal on lobster grounds has been banned in such places as Africa and Australia (Matthews, 1962; Chittleborough, 1974; Hancock, 1974).

To study the effects of offal on catches in the NWHI, field experiments were conducted by NMFS during Townsend Cromwell cruises TC-81-04 and TC-82-05 (Gooding, in preparation). In the first experiment during cruise TC-81-04 at Maro Reef, catch rates of baited pots with offal tied on the outside were compared with those of controls which were baited only. During this experiment the catch rates were 4.56 individuals/pot-night for the control and 0.13 individuals/pot-night for the experimental traps. At Necker, the catch rate for control traps was 0.97 individuals/pot-night and that for experimental traps was 0.19 individuals/pot-night.

During the second experiment on cruise TC-82-05, five stations produced catch rates from 0.08 to 2.31 individuals/pot-night for controls whereas those obtained from the experimental traps ranged from 0.00 to 0.06 individuals/pot-night. Data from one station were not used in the analysis due to effects produced by rough seas resulting in heavy gear losses and zero-catch rates.

The experiments demonstrated that the presence of offal in or around the pots substantially decreases catch rates for *P. marginatus* in the NWHI.

PREDATORS

Among the management measures adopted for the spiny lobster fishery in Hawaii is the prohibition of retaining berried female and sublegal-sized lobsters. The usual practice aboard commercial boats is to sort out the berried female and sublegal-sized lobsters as the traps are retrieved and to return them to the water as quickly as possible. At the same time, the fishermen remove and discard the old bait and replenish the container.

What happens to lobsters that have been caught and released is of considerable importance to the fishery. Gooding (1979, in preparation) noted that when berried and sublegal-sized lobsters were hauled aboard a boat and later released, they are subjected to considerable stress, resulting primarily from long exposure to air and sunlight, rough handling, release over unsuitable or unfamiliar territory, disorientation, and predators.

Because used bait is discarded as a vessel moves along the string of traps, predators are easily attracted to the stern; thus, discarded bait as well as surface-released lobsters are both consumed. To determine the degree of this type of predation and to identify the predators, the Honolulu Laboratory conducted field experiments during cruises TC-79-02 and TC-81-04, as well as during the *Easy Rider* charter cruise ER-80-01.

Casual observations on several research cruises and those made by commercial fishermen indicated that there were at least two principal predators -- the hon-ulua (*Caranx ignobilis*) and the galapagos shark (*Carcharhinus galapagensis*). Gooding (1979) reported that predators such a omilu (*Caranx melampygus*), hon-ulua, reef whitetip shark (*Triaenodon obesus*), and gray reef shark (Carcharhinus amblyrhynchos) were seen near the NMFS vessel but none showed any inclination to prey on surface-released lobsters. Likewise, on cruise ER-80-01, potential predators such as hon-ulua, galapagos shark, tiger shark (Galeocerdo cuvieri), and ono (Acanthocybium solandri) were observed around the vessel but underwater observations revealed no predation on surface-released lobsters.

Results obtained during cruise TC-81-04, however, demonstrated conclusively that hon-ulua are voracious predators. Gooding (1982) concluded that the state of satiation is always a factor and that the number of lobsters consumed is directly related to predator size, predator school size, and size of lobsters released. Furthermore, Gooding's observations showed that bottom-release of lobsters, even on substrata that offers good shelter, does not ensure high survival in the presence of voracious predators. The only practical safeguard to ensure high survival was to release lobsters near the bottom in protective bags or containers and only when there was reasonable assurance that large schools of predators were not following the boat.

ECONOMIC STATUS AND POTENTIAL

In early 1977, following the discovery of commercial concentrations of spiny lobsters at Necker, five commercial vessels began full-scale trapping operations and by the end of the year had produced a catch of 31,547 kg from the NWHI, thereby catapulting the statewide landings of spiny lobster to more than 13 times the previous year's landings. This early beginning of the fishery was not without problems. The market structure was unorganized and the boats returning from the NWHI lobstering grounds faced a local market that was chaotic and unable to absorb the sudden heavy influx of live, whole lobsters. Ex-vessel prices averaged \$6.39/kg (\$2.09/lb) and the year's statewide catch of 37,659 kg was worth about \$240,600 to the fishermen.

The fishery experienced other "growing pains." Captains unfamiliar with transporting large numbers of live lobsters in their baitwells over the long distance from the NWHI lobstering grounds to Honolulu sometimes experienced losses of entire loads due to overcrowding and poor water circulation in the baitwells. Those vessels lucky enough to return with a full live load were faced with declining prices and attempted to maintain prices by marketing their catches in small amounts and over a longer period.

The chaotic market forced several marginal producers out of the fishery and by October 1977, only two vessels remained. These vessels continued to fish until October 1978 when they were joined by another entry into the fleet. The result was that landings from the NWHI declined to 12,440 kg, a 60 percent decrease from the previous year. The ex-vessel price, however, rose to \$6.60 kg (\$3.00/lb) making the 1978 statewide landings of 15,294 kg worth \$82,100 to the fishermen.

Also about this time, the industry began looking for other outlets for their products, particularly the frozen lobster tail export market. This new impetus raised the hopes of the industry and landings again rose, reaching 45,372 kg; however, only two vessels participated, and presumably almost all of the catch was from the NWHI. At an ex-vessel price of about $7.05/kg ($3.20/lb), the 1979 catch was worth $319,900. At-sea processing required large vessels not only with freezing capabilities but also with the ability to exert greater fishing pressure.

By 1980, the fleet was composed of three vessels, and among them they had the potential of setting and retrieving 2,500 lobster pots per night. This resulted in a catch of 148,907 kg worth $1.1 million at an ex-vessel price $7.49/kg ($3.40/lb).

Encouraged by the rising prices and continued strong demand for frozen lobster tails, the fishery continued to produce record catches. By 1981, the fleet had increased to 10 vessels, which caught a record 354,200 kg worth $2.7 million at an ex-vessel price of $7.71/kg ($3.50/lb).

Although catch records for 1982 are incomplete, the annual catch, produced by six vessels, is estimated to be 83,711 kg, down considerably from 1981. Ex-vessel prices advanced little to $8.06/kg ($3.60/lb), making the 1982 catch worth an estimated $674,714 to the fishermen.

Annual estimated landings with ranges of MSY are given below. Using the average CL of the males and females at Necker and Maro Reef (Table 3) and converting these to average weight using the length-weight relationships (Figure 8), an average weight of 533 g for both sexes combined was calculated. Based on this average weight, the range in MSY is estimated to be 106,600 to 231,855 kg.

The landings in 1977-79 were far below the lower range MSY. In 1980 and 1982, the estimated landings fell within the range of MSY but in 1981, the upper limit of the MSY was exceeded by about 122,000 kg.

When the fishery first began, some believed that the potential was as good as that of other lobstering grounds throughout the world. Potential production from the NWHI grounds based on extrapolations of initial catch rates seemed encouraging; however, as with many new, developing fisheries, once the initial stock was reduced by heavy fishing and catch rates declined, enthusiasm subsided. By then, our surveys demonstrated that the NWHI catch rates of spiny lobster were nowhere near those of the major lobster fisheries of the world, for example Australia and South Africa. Furthermore, in the NWHI fishery, risks were greater as vessels had to travel 1,700 nmi round trip to fish at Necker and Maro Reef, the only two grounds with commercial concentrations of spiny lobsters.

Even with the most optimistic projection, it is not likely that the NWHI spiny lobster stock could support more than a few full-time vessels. Furthermore, profitability may depend on a multispecies operation. Places such as Nihoa, Pearl and Hermes Atoll, Gardner Pinnacles, and Midway can probably be fished profitably in combination with other types of fishing. Examples are bottomfishing for members of the snapper-grouper complex, trolling for coastal pelagic species such as wahoo (*Acanthocybium solandri*), and trapping for deepwater caridean shrimps. There are also several important species in the by-catches of lobster pots such as slipper lobsters (*Scyllarides squammosus* and *S. haani*) and frog or kona crab (*Ranina ranina*) which could add to a vessel's profitability.

MANAGEMENT GUIDELINES

Management of the spiny lobster fishery in Hawaii is achieved through a series of regulations which apply to two permit areas. Permit Area 1 encompasses the U.S. fishery conservation zone (FCZ) around the NWHI or all islands and banks west of long. 161° 00'W. Permit Area 2 includes the main Hawaiian islands or those islands and banks in the archipelago east of long. 161° 00'W.

Currently the management measures published in the Federal Register[3] include the following:

> Size regulation. Whole lobsters of 77.0-mm CL or greater may be retained. If the CL cannot be determined, only lobsters with tails at least 50 mm wide may be retained, except for an allowance of up to 15 percent of the catch, by number, which may include tail widths between 45 and 49 mm.
>
> Reproductive condition restrictions. Berried females may not be retained or stripped of eggs attached to the pleopods.
>
> Closed areas. Spiny lobster trapping is not allowed within 20 nmi of Laysan and within the FCZ landward of the 10-fathom curve as depicted on National Ocean Survey charts 19022, 19019, 19016.
>
> Gear restrictions. Spiny lobsters may be taken only with lobster pots or by hand. Other gears or chemical agents are prohibited. Furthermore, pot entrance may measure no more than 26.7 cm (10.5 in) at its greatest

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[3] Federal Register 47(126), June 30, 1982, contains the proposed rule; Federal Register 48(26), February 7, 1983, contains the final rule. The final rule contains no substantial changes from the proposed rule except minor revisions.

diagonal or diameter at the larger end and no more than 16.5 cm (6.5 in) at its greatest diagonal or diameter at the smaller end.

Permits. Any U.S. vessel trapping commercially in the NWHI management area (Permit Area 1) must have a permit issued by the director, Southwest Region, NMFS.

Recordkeeping and reporting. The operator of any vessel engaged in lobster trapping operations in Permit Area 1 shall maintain an accurate and complete logbook furnished by NMFS, recording all information as required.

Landing requirements. The operator of a fishing vessel that has fished in Permit Area 1 shall contact by radio or otherwise, an authorized officer at least 24 hours before landing and report to this officer the port, date, and time of unloading. An authorized officer is defined as any commissioned, warrant, or petty officer of the U.S. Coast Guard (USCG); a special agent of the NMFS; any officer designated by the head of any federal, state, or territorial agency which has entered into an agreement with the Secretary of Commerce and the Secretary of Transportation to enforce the provisions of the Magnuson Fishery Conservation and Management Act; and any USCG personnel accompanying and acting under the direction of any USCG commissioned, warrant, or petty officer.

Experimental fishing. The Secretary of Commerce may authorize experimental fishing for spiny lobster which would otherwise be prohibited. A NMFS scientific observer must be aboard the vessel while the vessel is engaged in such activity.

An additional provision of the regulations applies to protective measures established for the Hawaiian monk seal (Monachus schauinslandi) which was designated a depleted species under the Marine Mammal Protection act and listed as an endangered species effective November 23, 1976. Briefly, these measures specify that in the event that a monk seal dies from causes that appear to be related to the spiny lobster fishery, an investigation will be conducted by the director of the Southwest Region. If it is determined that the death is related to the spiny lobster fishery, emergency measures will be instituted, as required, to protect the monk seal population. In addition to the regulations established under the Spiny Lobster Fishery Management Plan, there are state laws and rules which are applicable to fishing for and landing of spiny lobsters and other crustaceans. State laws establish a seasonal closure, prohibit taking of ovigerous females, establish a minimum size, and prohibit the landing of lobsters from which the carapace and tail have been separated; however, the state law also provides that such measures shall not apply if the catch was made outside of state waters and the possession or sale has been licensed (import permit) by the Hawaii Department of Land and Natural Resources.

SUMMARY

The investigation conducted by NMFS has elucidated several aspects of the spiny lobster resource in the NWHI. Particularly striking is the fact that P. marginatus is unevenly distributed and the only stocks which are of commercial potential are those at Necker and Maro Reef. The survey showed that the relative abundance of lobsters is highest at the 55 to 73 m depth in localities near the lower end of the NWHI chain and at the 19 to 54 m depth in those localities toward the northern end of the chain. Whereas a small female lobster from the NWHI may spawn just as many eggs as one in waters off Oahu, at larger sizes the NWHI female apparently spawns fewer eggs. The spawning season for NWHI populations is estimated to be all year at the lower end of the chain, peaking in summer. However, among the more northern localities, the spawning period is shorter and confined primarily to the summer months.

Studies on growth rate showed that a male lobster from Necker grows at about the same rate as one in waters around Oahu. For the Oahu stock, males mature at 63.6-mm CL whereas the females mature at 58.6-mm CL. For the stock at Necker, males mature at 59.2-mm CL and females at 60.7-mm CL. The difference between localities is not significant.

Lobsters tend to avoid baited traps in the presence of offal. Large schools of predators can inflict serious losses among surface-released berried and sublegal-sized lobsters.

The lobsters at Necker and French Frigate Shoals are, on the average, smaller than those found elsewhere in the chain. The legal to sublegal size ratio of the catch showed wide variation with no particular trend. The sex ratio of the stocks, however, showed that among the legal-sized lobsters in the catch, males predominated. Among sublegal-sized lobsters, however, there was a preponderence of females at most localities.

A legal-sized lobster of 77.0-mm CL weighs about 378.1 g, whereas a legal-sized female is heavier, weighing 402.4 g. There is sexual dimorphism in the growth pattern.

The relationship between CL and tail weight predicts a legal-sized male would have a tail weight of 130 g and a female 156 g.

Discriminant analysis based on tail width correctly classifies 94.8 percent of the sublegal-sized and 85.8 percent of the legal-sized lobsters. The tolerance factor adopted for the fishery management plan is that no more than 15 percent of the total number of tails landed may be less than the specified tail width limit of 50 mm.

Studies on population dynamics provided a range of possible MSY of from 200,000 to 435,000 lobsters/year.

Experiments on gear competition showed that pot spacings of between 35 and 46 m produced the highest catch rates. Tests with escape gaps revealed that the overall escape rate of sublegal-sized animals was about 60 percent. Studies on ghost fishing of lost traps demonstrated that they continue to attract lobsters and, over the short term, continue to fish; however, over the long term, lobsters appear to escape through trap entrances.

Finally, the investigation showed that even with the most optimistic projections, it is not likely that the NWHI lobster fishery will expand significantly over the next few years. The upper limit of the MSY was exceeded in 1981. With reduced catch rates at this time, it is not likely that the present scale of production can support more than a few vessels. The future of the fishery will depend to a large extent on the operation of multispecies fishing boats that can participate in other fisheries being developed in the NWHI.

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Groundfish Fisheries and Research in the Vicinity of Seamounts in the North Pacific Ocean

RICHARD N. UCHIDA and DARRYL T. TAGAMI

Introduction

In the central and western North Pacific Ocean, one of the chief topographic characteristics of the ocean floor is the large submarine volcanoes, which were once high islands. Some of these former volcanic islands are now worn down into low, sandy atolls such as Kure Atoll in the Hawaiian Archipelago (Menard and Hamilton, 1963; Carlquist, 1970). However, many others have subsided 0.5 km or more below the sea surface and their summits lack a coral cap. These are the guyots or seamounts identifiable as former islands by their form and by the presence of shallow-water fossils that have been dredged from their summits. By definition, a seamount is an elevation that rises 1,000 m or more from the sea floor and is flat and of limited extent across the summit (U.S. Board on Geographic Names, 1969).

The Hawaiian Archipelago and the numerous seamounts to the north and northwest of the chain are shown in Figure 1. Those to the north are the Musicians Seamounts which have summits that are rather deep, most of them well over 1,650 m below the sea surface. The seamounts discussed in this report lie on the Hawaiian and Emperor Seamount Ridges. The Hawaiian Ridge extends for some 1,350 n.mi. from the Island of Hawaii on the southeastern extremity to Kure Atoll on its northwestern end. The Emperor Seamount Ridge then continues in a northerly direction and terminates at the juncture of the Aleutian and Kurile Islands arc and trench systems (Malahoff and Woollard, 1970).

The 200-mile Fishery Conservation Zone (FCZ) around the Hawaiian Archipelago includes the Northwestern Hawaiian Islands (NWHI), a chain of small islands stretching from Nihoa to Kure Atoll. Surrounding these islands are numerous submerged banks and seamounts, including Hancock Seamounts, which in recent years have been fished by Japanese trawlers under a quota established by the preliminary management plan (PMP)[1] for seamount-groundfish resources.

In October 1976, just 5 months before enactment of the Magnuson Fishery Conservation and Management Act (MFCMA), the Honolulu Laboratory of the Southwest Fisheries Center (SWFC), National Marine Fisheries Service (NMFS), launched an investigation of the marine resources of the NWHI. Because the extent of the investigation was beyond the capabilities of the staff and facilities of any single research agency in Hawaii, the SWFC proposed a cooperative effort with the Hawaii Division of Aquatic Resources (HDAR), Hawaii Department of Land and Natural Resources, and the U.S. Fish and Wildlife Service (USFWS). From the proposal evolved a formal tripartite agreement which, in effect, gave responsibility to the HDAR for the survey and assessment of the inshore fishery resources and to the USFWS for land-associated resources such as sea and land birds. The SWFC assumed responsibility for developing a quantitative fishery survey and assessment of the slope, coastal pelagic, and seamount resources. A short time after the agreement was signed, a fourth agency, the University of Hawaii Sea Grant College Program, became an active participant in the investigation by assuming responsibility for research to fill obvious gaps in the tripartite investigation.

This report reviews the historical de-

ABSTRACT—The trawl fishery over the central North Pacific seamounts expanded rapidly after 1967 when exploratory fishing by Soviet trawlers demonstrated commercial concentrations of pelagic armorhead, Pentaceros richardsoni, *and smaller quantities of alfonsin,* Beryx splendens. *In 1969, Japanese trawlers entered the fishery but developmental problems led to wide catch fluctuations in 1969-71. After 1971, catches stabilized and then peaked at 34,538 metric tons in 1974.*

Hancock Seamounts, within the 200-mile U.S. Fishery Conservation Zone around the Hawaiian Archipelago, were fished in 1972-76 by Japanese trawlers, producing annual catches from 653 to 8,518 metric tons. In 1978-81, U.S. observers accompanied three Japanese trawlers which made six trips to Hancock Seamounts. Observer data indicated that the pelagic armorhead stock had recovered to some extent from the intense fishing prior to 1977. The catch per unit of effort in 1980 and 1981 improved and showed an upward trend.

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[1] Southwest Region, National Marine Fisheries Service, NOAA, Terminal Island, California. Final environmental impact statement/ Preliminary fishery management plan. Seamount groundfish fishery resources (pelagic armorheads and alfonsins). NOAA, NMFS, January 1977, 27 p.

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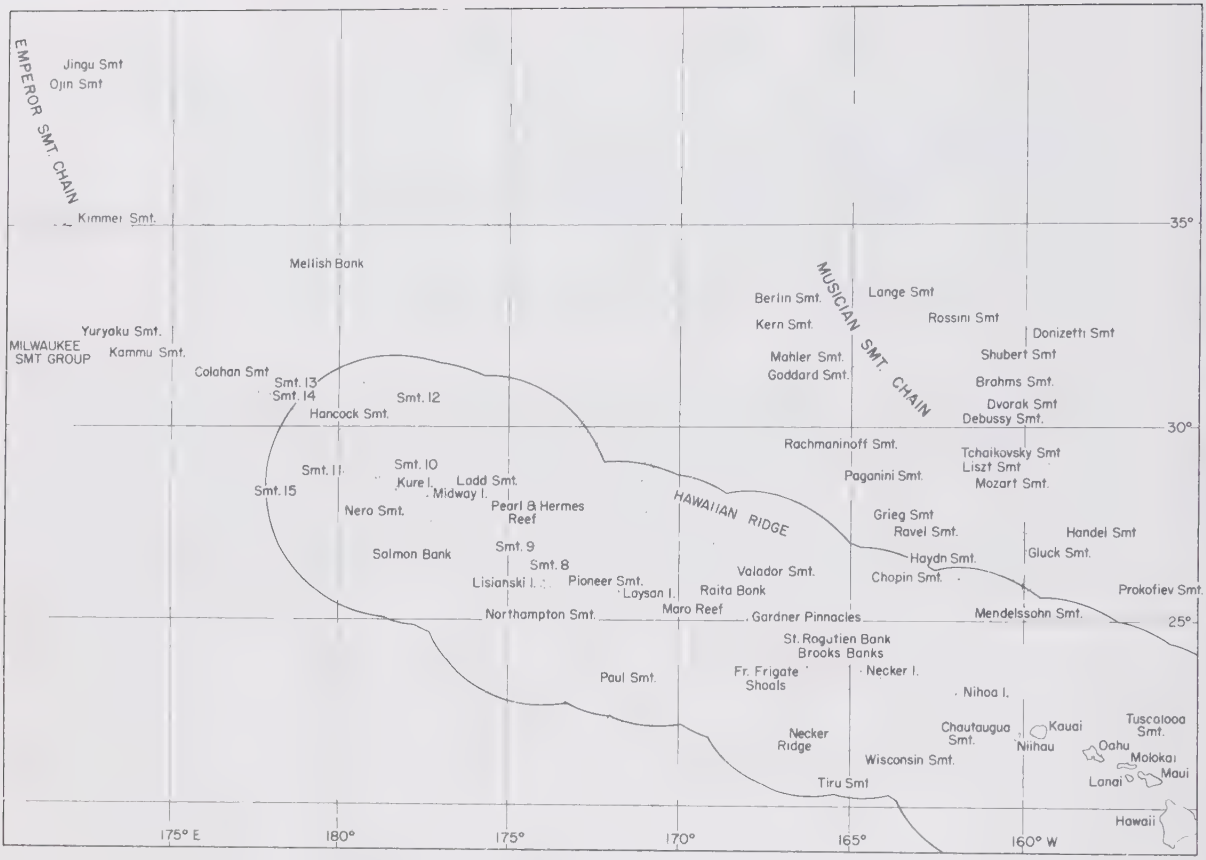
EMPEROR SMT. CHAIN
Jingu Smt
Ojin Smt
Kimmei Smt.
35°
Mellish Bank
MUSICIAN SMT. CHAIN
Berlin Smt.
Lange Smt
Kern Smt.
Rossini Smt
Donizetti Smt
Yuryaku Smt.
MILWAUKEE SMT GROUP
Kammu Smt.
Mahler Smt.
Goddard Smt.
Shubert Smt
Colahan Smt
Smt. 13
Smt. 14
Smt. 12
Hancock Smt.
Brahms Smt.
Dvorak Smt
Debussy Smt.
30°
Rachmaninoff Smt.
Tchaikovsky Smt
Liszt Smt
Mozart Smt.
Smt. 11
Smt. 10
Kure I.
Ladd Smt.
Midway I.
Smt. 15
Paganini Smt.
HAWAIIAN RIDGE
Nero Smt.
Pearl & Hermes Reef
Grieg Smt
Ravel Smt.
Handel Smt
Salmon Bank
Smt. 9
Smt. 8
Haydn Smt.
Gluck Smt.
Valador Smt.
Chopin Smt.
Lisianski I.
Pioneer Smt.
Laysan I.
Raita Bank
Prokofiev Smt.
Northampton Smt.
Maro Reef
Gardner Pinnacles
Mendelssohn Smt.
25°
St. Rogatien Bank
Brooks Banks
Paul Smt.
Fr. Frigate Shoals
Necker I.
Nihoa I.
Necker Ridge
Chautaugua Smt.
Kauai
Niihau
Tuscaloosa Smt.
Oahu
Molokai
Wisconsin Smt.
Lanai
Maui
Tiru Smt
Hawaii
175° E
180°
175°
170°
165°
160° W

Figure 1.—Hawaiian Archipelago and nearby seamount chains and groups.

velopment of the seamount-groundfish trawl fishery over the central North Pacific seamounts, presents an analysis of the data collected by U.S. observers on Japanese trawlers fishing over Hancock Seamounts in 1978-81, and describes the results of the SWFC's surveys over the seamounts within the FCZ around the Hawaiian Archipelago. An earlier report described the exploratory survey at Hancock Seamounts from October 1976 through May 1979 (Gooding, 1980).

Description of the Fishery

History

The historical development of the seamount-groundfish fishery in the central North Pacific has been described in detail by Chikuni (1970, 1971b), Sakiura (1972), Sasaki (1974), and Takahashi and Sasaki (1977). Until 1967, the seamounts aroused very little interest because most fishery scientists were unaware of the resources associated with them.

The U.S.S.R. was the first nation to commercially exploit the seamount-groundfish resources in this area. In November 1967 a Soviet commercial trawler discovered large concentrations of pelagic armorhead, *Pentaceros richardsoni*, on the Emperor Seamount Chain which led to an almost immediate exploitation of the resource by the Soviet trawling fleet and prompted further exploratory fishing on seamounts closer to the Hawaiian Archipelago including Kimmei Seamount, the Milwaukee Seamount group, and Hancock Seamounts (Sakiura, 1972).

The initial catches of the Soviet trawlers were impressive: As much as 20-30 metric tons (t) were taken in hauls of 10-20 minutes (Sakiura, 1972). The catch rate averaged 5.8 t per half-hour tow in 1968 and doubled to 11.7 t per half-hour tow in 1969. Furthermore, in one 8-month period from December 1969 to July 1970, Soviet trawlers reportedly harvested 133,400 t of pelagic armorhead from the seamounts. A second species of commercial value, the alfonsin, *Beryx splendens*, made up as much as 30 percent of some of the trawl hauls. The Soviet trawlers reported that the thickness of the schools of pelagic armorhead over the seamounts was as much as 160 m but usually was closer to 30 m. The size of the catches reported by the Soviets, however, was questioned by Sakiura (1972).

In August 1969, Japanese trawlers of 1,500-4,000 gross tons entered the fishery. Their initial effort was mostly exploratory, but they set the stage for full-scale commercial operations by 1972. Frequently, some trawling was conducted by Japanese trawlers en route to and from the Bering Sea and the Gulf of Alaska. To assist in the development of the fishery, Japanese research vessels conducted extensive surveys in 1972 to determine the distribution of pelagic armorhead and alfonsin and their potential for development. They explored the central North Pacific for uncharted seamounts, verified the positions of known seamounts, produced charts on the topography and profile of most of the seamounts, and collected oceanographic data to determine the physical, chemical, and biological characteristics of the waters in the vicinity of these seamounts (Japan Marine Fishery Resource Research Center (JAMARC), 1973; Japan Fisheries Agency, 1974). Additional surveys followed in 1973 and 1974. Results of these surveys showed that many of the seamounts were too deep for effective trawling. Those suitable for trawling were located on the southern end of the Emperor Seamount Chain, beginning with Kimmei Seamount and extending south-southeast to Hancock Seamounts in the U.S. FCZ (Sasaki, 1978).

When first marketed in Japan, the pelagic armorhead met stiff consumer resistance and the fishing firms temporarily suspended trawling owing to poor sales (NMFS, 1975). Extensive advertising and sales promotion, however, boosted market demands. By 1973, consumer demand was on an upward trend and the Japanese trawlers expanded their operations over Milwaukee, Colahan, and Hancock Seamounts, but the catch rates were already declining. In 740 hours of trawling in 1973, the catch rate was 33.8 t per hour, down considerably from the 1972 catch rate of 60.1 t per hour (Takahashi and Sasaki, 1977). A strong surge in demand in early 1975 continued into 1977, but landings remained low (NMFS, 1977).

Historical Japanese Catches

Because the early years (1969-71) of the Japanese seamount-groundfish trawl fishery were exploratory and developmental, annual catches fluctuated widely; 1972 is regarded as the real beginning of the commercial fishery.

The annual catch, trawling effort, and catch per unit of effort (CPUE) of pelagic armorhead for all the major seamounts fished by the Japanese in 1969-76 are given by Takahashi and Sasaki (1977). The Milwaukee Seamount group was by far the most productive, accounting for nearly 55 percent of the 1969-76 catch. Next in importance was Kimmei which produced 17 percent of the pelagic armorhead catches, followed by Colahan, Hancock, C-H (unnamed seamount located between Colahan and Hancock), "others," and Mellish. The relative abundance of pelagic armorhead was highest at Hancock, followed closely by Colahan and C-H (discounting Mellish because of the small effort there). These were followed by Milwaukee, "others," and Kimmei.

From 1969 to 1971, Japanese landings of pelagic armorhead fluctuated widely between 3,280 t in 1969 and 30,047 t in 1970; however, from 1972 to 1976, the catches stabilized, fluctuating between 18,952 t in 1975 and 34,538 t in 1974. Effort, on the other hand, increased from 157 to 2,807 hours during the exploratory phase, dropped to 496 hours in 1972, then rose steadily thereafter to 2,667 hours in 1976, an increase of more than five times during the latter period. The result was that the CPUE declined steadily from the 1972 peak of 60.2 t per hour to 9.7 t per hour in 1976[2] (Fig. 2). Figure 2 also shows the catch statistics (discussed later in greater detail) for three Japanese trawlers that fished Hancock in 1978-81 after the enactment of the MFCMA.

Because Hancock Seamounts fall within the U.S. FCZ, it is of interest to compare the catch and trawling effort over them with the total central North Pacific catch and effort. The Japanese commercial trawling effort at Hancock Seamounts in 1972-76 varied from 24 to 212 hours and averaged 74.6 hours (Takahashi and Sasaki, 1977). Hancock Seamounts received from <1 to 29 percent of the entire central North Pacific trawling effort. Catches made during the same period varied between 653 and 8,518 t and averaged 2,804 t. The landings from Hancock constituted from 3 to 34 percent of the entire central North Pacific seamount landings. Catches at Hancock were usually <7 percent of the total central North Pacific landings, but the 1973 catch was slightly more than one-third of the 25,047 t landed by the Japanese trawlers, because there was a drastic decline in catches that year at Milwaukee Seamount, which normally contributed the largest proportion of the pelagic armorhead catches from the central North Pacific seamounts.

Although the seamount fishery concentrated on pelagic armorhead, a small amount, usually <5 percent of the catch, included a second species of commercial value, the alfonsin. The annual Japanese catches of alfonsin from the central North Pacific seamounts varied widely from 26 to 2,807 t during 1969-71. Between 1972 and 1976, the catches fluctuated from 0 in 1974-75 to 1,726 t in 1976[3]. Overall, from 1969 to 1976, <2 percent of the catches were alfonsin (excluding other miscellaneous species taken by the trawl). Kimmei Seamount was by far the most productive for alfonsin, accounting for about 69 percent of the landings, followed by the Milwaukee Seamount group which produced 24 percent of the landings. The remaining seamounts, all south of Milwaukee (except, perhaps, for some unknown location in the "others" group), contributed about 3 percent or less of the total landings. Kimmei also had the highest catch rate of alfonsin, 0.6 t per hour, far better than at Hancock which had the second highest catch rate of 0.1 t per hour. The data suggest that the center of abundance of alfonsin in the central North Pacific is near Kimmei whereas that for pelagic armorhead is more to the south near Colahan, C-H, and Hancock Seamounts.

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[2] Unpublished data obtained through the courtesy of Takashi Sasaki of the Far Seas Fisheries Research Laboratory, Japan Fisheries Agency, indicated that the catch rates declined 2.4 per hour in 1977 and fluctuated within a narrow range of 0.3 and 0.8 per hour in 1978-81. Trawling effort ranged from 1,631 to 2,642 hours during 1977-81 while total catch varied between 500 and 6,245 t.

[3] Unpublished data from the source cited in footnote 2 indicated that the 1977-81 catch varied between 1,649 and 8,638 t with CPUE fluctuating between 0.7 and 4.8 t per hour. The trawling effort remains the same as noted in footnote 2.

In addition to trawls, alfonsin are caught by bottom longlines. The Japanese bottom longline fishery for this species began on the Milwaukee Seamount group in 1972. At present, virtually nothing is known about this so-called "open fishery" because no permits or licenses are required in Japan. Information provided by the fishing master of the FV *Biko Maru*, a bottom longliner, revealed that the alfonsin resource over the central North Pacific seamounts appears to be declining (Suisan Sekai, 1976). Furthermore, fishing intensity has increased over the years with more Japanese and Korean vessels entering the fishery. The result was that whereas a full load could be obtained in as few as 13 days in previous years, many boats nowadays are not only forced to stay on the grounds longer, but also, to fish for other less desirable species such as rockfish or "akodai," *Sebastes matsubari*, to make up for the lack of alfonsin.

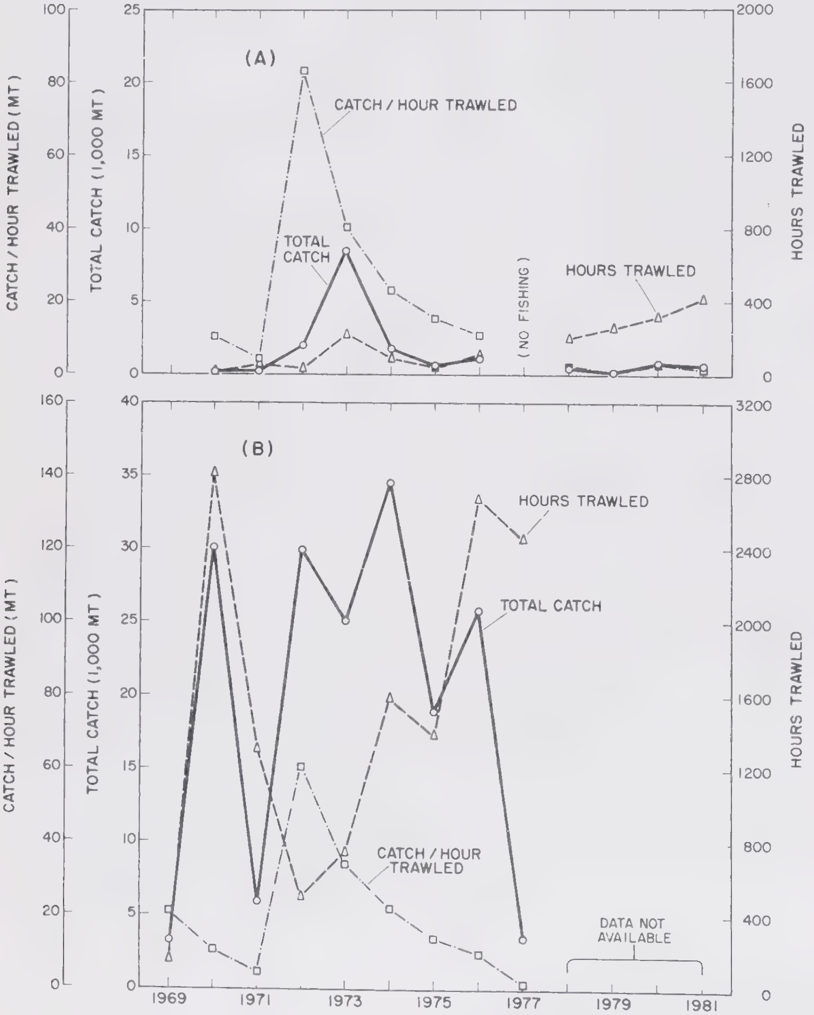

Figure 2.—Catch, hours trawled, and catch per hour trawled in the Japanese trawl fishery for pelagic armorhead over (A) Hancock Seamounts and over all the (B) central North Pacific Seamounts, 1969-81 (data for 1969-76 are from Takahashi and Sasaki, 1977).

Fishery at Hancock Seamounts

Because a fishery management plan (FMP) for pelagic armorhead and alfonsin has not been prepared, temporary measures were set forth in a PMP for the seamount-groundfish fishery resources within the U.S. FCZ around the Hawaiian Archipelago. The regulations temporarily restrict the foreign harvest to a 2,000 t catch quota by trawling or bottom longlining and to 60 vessel-days of effort, and, in addition, establish a licensing procedure for foreign vessels, require the submission of detailed catch and effort data, and placement of U.S. observers on any foreign fishing vessel.

In 1978, an application submitted by JAMARC for a trawling survey at Hancock Seamounts was approved. Since then, two commercial trawlers have received approval to fish at Hancock. Each trip, including the survey conducted in 1978, was accompanied by a U.S. observer who collected detailed data on catch by species and fishing effort, and measured and weighed representative samples of the catch. As time permitted, the observers made observations on food and feeding habits and on gonad condition[4].

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[4] Seamount fishery, foreign vessel observer reports, available as Southwest Fisheries Center Administrative Reports at the SWFC Honolulu Laboratory, NMFS, NOAA, Honolulu, HI 96812: T. K. Kazama. 1978. *Ryuyo Maru No. 2* (22 April-3 June 1978). SWFC Admin. Rep. 15H, 10 p. G. C. Evering. 1979. *Aso Maru* (27 May-10 July 1979). SWFC Admin. Rep. H-79-14, 10 p. A. R. Everson. 1980. *Kitakami Maru* (9 August-4 October 1980). SWFC Admin. Rep. H-80-15, 13 p. A. R. Everson. 1980. *Aso Maru* (24-30 September 1980). SWFC Admin. Rep. H-80-16, 10 p. N. T. Shippen. 1981. *Aso Maru* (9-19 June 1981). SWFC Admin. Rep. H-81-4, 8 p. W. B. Barnett. 1981. *Kitakami Maru* (15 August-1 October 1981). SWFC Admin. Rep. H-81-9, 12 p.

Table 1.—Vessel specifications and other statistics of Japanese independent stern trawlers fishing for pelagic armorhead at Hancock Seamounts, 1978-81.

Item	Vessel code A	 B	 C
Vessel specifications			
Length (m)	56.62	91.60	95.11
Gross ton	549.86	2,961.07	3,608.29
Net ton	215.92	1,501.27	1,968.81
Width (m)	9.20	15.50	16.00
Draft (m)	4.15	6.50	9.80
Engine type	Diesel	Diesel	Diesel
Horsepower	1,500	4,000	3,900
Company/owner	Nippon Suisan, Ltd.	Hokkaido Gyogyokosha	Nippon Suisan, Ltd.
Year commissioned	1966	1967	1964
Home port	Konmon-Ko, Tobata	Tokyo Harbor	Konmon-Ko, Tobata
Personnel (no.)			
Officers	9	10	9
Crew	25	40	41
Total	34	50	50

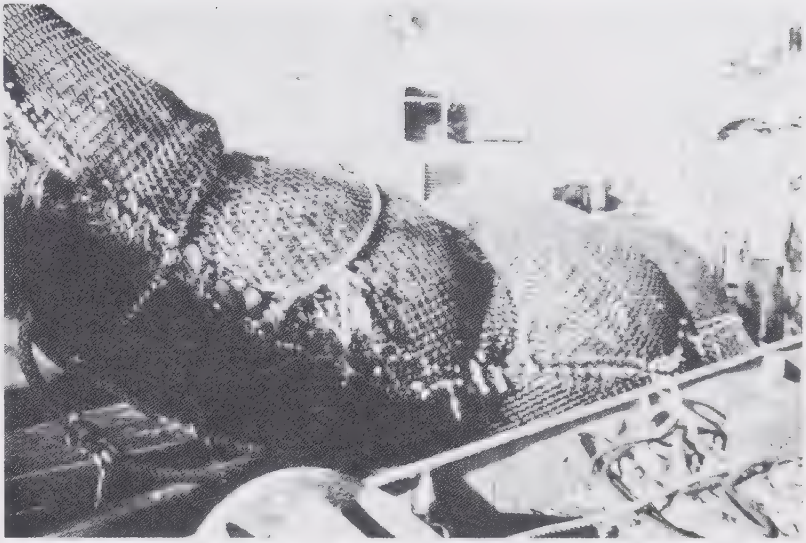

Figure 3.—The cod end of a trawl holding an estimated 7,000 kg of pelagic armorhead and alfonsin aboard Vessel A.

Table 2.—Dimensions of trawl doors and nets used on Japanese trawlers fishing at Hancock Seamounts, 1978-81.

Item	Vessel code A	 B	 C
Trawl doors			
Shape	Rectangular	Rectangular	Rectangular
Type	Longitudinal	Concave	Longitudinal
Dimensions (m)	2.0 × 3.0	2.7 × 4.3	2.2 × 4.4
Weight (kg)	1,200	4,167	3,100
Nets			
Dandyline (m)	80	150	120
Headrope (m)	28.0	46.0	50.5
Footrope (m)	40.0	59.4	59.0
Vert. opening (m)	6	6	6
Horiz. opening (m)	16	14	22
Warp length (m)	700	1,200	800
Floats			
Number used	30-36	36	46-50
Size (mm)	300-360	360	300-360
Material	Cycolac	Plastic	Cycolac
Shape	Round	Round	Round
Bobbins			
Number used	23	114	35
Size (mm)	530	540-580	530
Material	Rubber; iron	Steel; rubber	Rubber; iron
Shape	Round	Round (car tires)	Round
Mesh size			
Wing (mm)	240	240	180
Square (mm)	180	50/90	150
Belly (mm)	150/120	50/90	150, 120, 90
Cod end (mm)	90	90	90

The three trawlers that fished at Hancock Seamounts fell into two of three basic types licensed by Japan (Nelson et al., 1981). Vessel A[5], in the first class of small, independent trawlers, can process the catch into frozen products but cannot produce fish meal and oil. A cod end full of fish caught on Vessel A is shown in Figure 3. Vessels B and C belong to the third class of large freezer trawlers and can produce frozen products as well as fish meal and oil. Vessel specifications and other data are given in Table 1, and description of the trawling gear is given in Table 2. Data on the catch of pelagic armorhead, alfonsin, and other miscellaneous species, number of hauls, total trawling time, average time per haul, and CPUE for all trips to Hancock Seamounts by the three trawlers are given in Table 3. No adjustment was made to standardize the effort unit to account for possible differences in fishing power between the two classes of trawlers. Usually, fishing power is proportional to the gross tonnage of the vessel or to the engine horsepower. However, because neither Vessel B nor C fished the same stock at the same time and place as did Vessel A, comparison of fishing power could not be attempted.

We did find it necessary, however, to adjust the total fishing time for Vessel B to make the effort unit comparable with those of the other vessels. For Vessel B, effort (fishing time) was based on bottom time of the trawl, whereas for Vessels A and C, effort included not only the actual bottom trawling time, but also, the time required for the net to reach the bottom, ascend to the surface, and the turnaround time, because these vessels usually made several passes over the seamount before haulback to empty the net. The turnaround is accomplished by raising the doors completely out of the water and fastening them to the gallows. Then, with the net still in the water and streaming aft, the vessel is turned and positioned for another pass. Admittedly, the measure of effort is not precise. The fact that Vessel B was operating under a charter with JAMARC and that the others were commercial trawlers may explain the discrepancy in the way effort was calculated.

In 1978, the catch rate (adjusted) rose to 2.1 t/hour, then declined in 1979 to 0.7 t/hour, the lowest level at Hancock since fishing began there in 1970. Fish-

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[5] To preserve anonymity of the Japanese trawlers that fished over Hancock Seamounts, the vessels are identified with code letters.

Table 3.—Catch of (in metric tons) pelagic armorhead, alfonsin, and other species, number of hauls, total trawling time, average time per haul, and catch per hour of three Japanese trawlers that fished over Hancock Seamounts, 1978-81.

						Catch					Adjusted		
Seamount	Vessel code	Cruise dates	No. of hauls	Total trawling time[1] (min.)	Time per haul (min.)	Pelagic armorhead (t)	Alfonsin (t)	Others (t)	Total catch (t)	Catch per hour[2] (t)	Total trawling time[3] (min.)	Time per haul (min.)	Catch per hour
NW Hancock	B	4/22-6/3/78	39	335	8.6	178.3	1.3	1.8	181.4	32.5	3,822	98.0	2.8
SE Hancock	B	4/22-6 3 78	62	1,662	26.8	228 8	2.4	3.8	235.0	8.5	8 041	129.7	1.8
Total			101	1,997	19.8	407.1	3.7	5.6	416.4	12.5	11,863	117.4	2.1
NW Hancock	C	5/27-7/10/79	57	5,595	98.2	67.6	7.2	23.7	98.5	1.0			
SE Hancock	C	5/27-7/10/79	69	9,570	138.7	67.0	10.7	2.1	79.8	0.5			
K Bank	C	5/27-7/10/79	12	223	18.6	0.9	6.8	0.3	8.0	2.2			
Total			138	15,388	111.5	135.5	24.7	26.1	186.3	0.7			
NW Hancock	A	8/9-10 4/80	59	5,050	85.6	192.9	7.8	4.6	205.3	2.4			
NW Hancock	C	9/24-9/30/80	20	1,925	96.2	40.2	1.6	3.3	45.1	1.4			
SE Hancock	A	8/9-10/4/80	102	9,650	94.6	461.1	23.7	14.1	498.9	3.1			
SE Hancock	C	9/24-9/30/80	14	2,190	156.4	40.5	0.9	4.0	45.4	1.2			
K Bank	A	8/9-10. 4/80	2	10	5.0	0.0	0.2	0.2	0.4	2.4			
Total			197	18,825	95.6	734.7	34.2	26.2	795.1	2.5			
NW Hancock	C	6/9-6/19/81	19	1,885	99.2	118.0	8.7	5.8	132.5	4.2			
NW Hancock	A	8/15-10/1/81	155	10,522	67.9	164.7	5.8	8.7	179.2	1.0			
SE Hancock	C	6/9-6/19/81	25	2,250	90.0	259.3	11.2	3.0	273.5	7.3			
SE Hancock	A	8/15-10/1/81	118	9,799	83.0	34.7	8.6	7.2	50.5	0.3			
K Bank	C	6/9-6/19/81	5	70	14.0	12.1	0.0	< 0.1	12.1	10.4			
K Bank	A	8/15-10/1/81	34	171	5.0	9.0	3.6	1.3	13.9	4.9			
Total			356	24,697	69.4	597.8	37.9	26.0	661.7	1.6			

[1] Total trawling time on Vessel B based on bottom time of the trawl; those for Vessels A and C based on total time the gear was in the water.

[2] No adjustment made for differences in fishing power of the trawlers

[3] Adjusted by using data from Vessel C which was similar in vessel characteristics to Vessel B. Adjustment made by calculating an overall time per haul for Vessel A for each of the seamounts fished and multiplying those values by the number of hauls made by Vessel B to obtain the total adjusted trawling time

ing improved significantly in 1980, particularly for the first vessel trawling at Hancock that year, Vessel A, which had a catch rate of 2.7 t/hour, or nearly four times that of the previous year. Fishing continued to improve in 1981 when the first vessel fishing Hancock, Vessel C, had a catch rate of 5.6 t/hour, or more than twice that for Vessel A in 1980.

In 1980 and 1981, it was obvious that the stock was reduced drastically by the first vessel that fished earlier in the year; the second vessel to arrive on the scene invariably experienced poorer fishing. In 1980, Vessel A, which operated at Hancock Seamounts from 9 August to 4 October, had relatively good catch rates at Northwest (NW) Hancock, Southeast (SE) Hancock, and at K Bank (Table 3). However, Vessel C, which fished after Vessel A from 24 to 30 September, experienced poor catches at NW and SE Hancock. Similarly, in 1981, Vessel C fished Hancock Seamounts from 9 to 19 June and made relatively good catches at NW and SE Hancock and K Bank, indicating that the stock had recovered from the previous year's fishing. When Vessel A arrived at Hancock Seamounts about 2 months later, however, the catch rates once again dropped to very low levels. The poor fishing of the second vessel at Hancock may have resulted from altered behavior or breakup of the pelagic armorhead school brought about by previous fishing activities or by changes in seasonal availability.

Of particular interest is the sharp increase in trawling effort which obviously occurred as a result of placing the pelagic armorhead and alfonsin stocks at Hancock under management (Fig. 2). For example, compared with effort at Hancock during the pre-MFCMA years, 1978 trawling effort reached an estimated 198 hours, or nearly as high as the 1973 peak of 212 hours. Furthermore, the increase in effort continued into 1979-81; effort in 1981 was 412 hours, nearly double the 1973 peak. However, the increase in effort was not accompanied by an increase in total catch, which tended to remain at less than 735 t, considerably below the 1,000 t allocated to Japan and the 2,000 t designated as the total allowable level of foreign fishing (TALFF) as set forth in the PMP.

Pelagic armorhead comprised 73-98 percent of the annual catch from 1978 to 1981. Alfonsin catches varied widely from 3.7 t in 1978 to 37.9 t in 1981, and comprised between 0.9 and 13.3 percent of the annual take in 1978-81.

Research Vessel Survey Results

From October 1976 to April 1981, surveys were conducted on nine cruises of the NOAA ship *Townsend Cromwell* to Seamounts 8, 9, 10, 11, Hancock, Ladd, and Nero (Table 4). These surveys were necessary not only to gather information on the status of the stocks at Hancock Seamounts but also to collect samples and data for studies on geographic distribution, species composition, size composition, food and feeding habits, age and growth, sexual maturity, and spawning.

Bottom Topography

Hancock Seamounts actually consist of two seamounts—one called Northwest (Fig. 4) and the other Southeast—

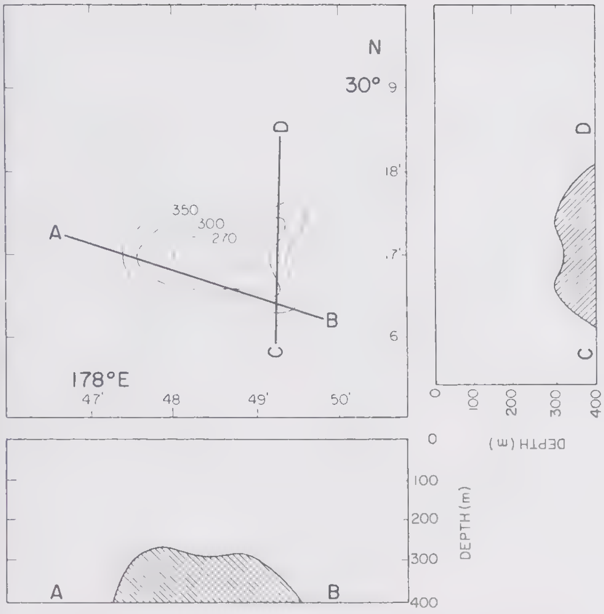

N
30° 9
18'
7'
6
178°E
47'
48
49'
50'
A
B
C
D
350
300
270
0
100
200
300
400
DEPTH (m)

Figure 4.—Bathymetry (m) and lateral profiles (A-B, C-D) of NW Hancock Seamount (from Japan Fisheries Agency, 1974).

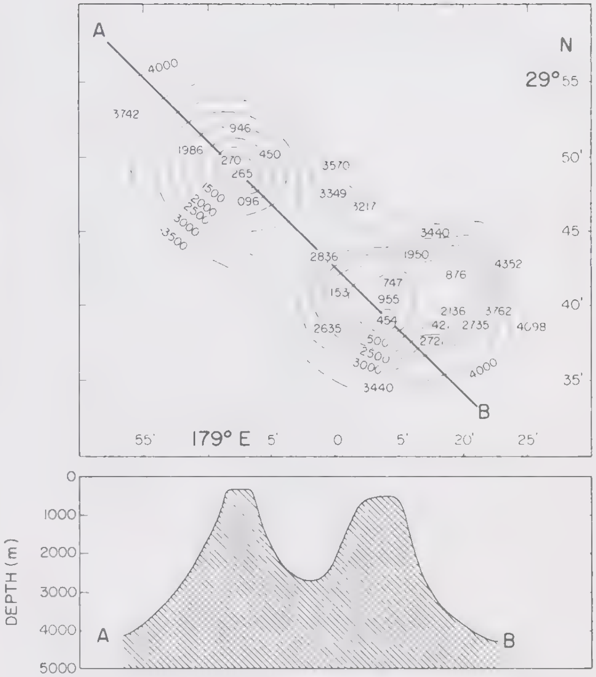

A
B
N
29°55
50'
45
40'
35'
55'
179° E
5'
0
5'
20'
25'
4000
3742
946
1986
270
450
265
3570
3349
3217
1500
2000
2500
3000
3500
096
3440
2836
1950
876
4352
747
153
955
454
2136
3762
42
2735
4098
2635
272
500
2500
3000
4000
3440
DEPTH (m)
0
1000
2000
3000
4000
5000

Figure 5.—Bathymetry (m) and lateral profile (A-B) of SE Hancock Seamount (from Japan Fisheries Agency, 1974).

separated by about 34 n.mi. The shallowest point on NW Hancock is 263 m; however, the north-south axis, which is the flat part of the seamount, is very narrow (0.5 n.mi.). Once past the flat portion, the slope is very steep on all sides (Japan Fisheries Agency, 1974).

SE Hancock (Fig. 5) consists of two summits. The summit on the northwestern end (Fig. 6) is flat, narrow, and 265 m at the shallowest area. The flat area extends for 1-2 n.mi., but beyond the 265 m depth contour, the bottom is steeply sloped. The southeastern side of this summit is sloped much more steeply than the northwestern side. The peak on the southeastern end of SE Hancock, also known as K Bank, is about 16 n.mi. to the southeast of the northwestern summit and is relatively rough; the shallowest point is 454 m deep (Japan Fisheries Agency, 1974). The summit of this peak was beyond the trawling depth capability of the *Townsend Cromwell*.

Table 4.—Seamount surveys of the *Townsend Cromwell*, October 1976-April 1981.

Cruise no.		Cruise period	Survey areas	Operations[1]		
				Trawl	Handline	Trap
76-06		10/12-11/21/76	SE Hancock and Seamount 10	X	X	—
77-02		5/12- 6/27/77	SE Hancock	X	X	—
78-01	(Part II)	1/16- 3/ 9/78	Seamount 11	—	X	X
78-03	(Part II)	9/ 6- 9/24/78	NW Hancock and Seamount 8	X	X	X
79-02	(Part II)	5/ 1- 6/ 6/79	NW and SE Hancock	X	X	X
80-02		3/24- 5/14/80	NW and SE Hancock, and Seamounts 9 and 11	X	X	X
80-03	(Part I)	5/28- 6/27/80	Ladd and Nero Seamounts	—	X	—
80-05	(Part II)	11/ 3-12/16/80	Ladd and Nero Seamounts	—	X	X
81-02		3/18- 4/23/81	SE Hancock and Ladd Seamounts	X	X	X

[1] X = conducted as part of cruise mission; — = not included in cruise mission.

Ladd Seamount, located about 50 n.mi. east-northeast of Midway Islands, is described as rather wide, flat, and about 64 m at the shallowest point (Fig. 7). There are, however, moderate amounts of outcroppings rising from the flat surface making the bottom quite irregular and rugged (Japan Fisheries Agency, 1974). The sides beyond the summit drop off very sharply.

Because of the lack of adequate bathymetric data on Nero Seamount (Fig. 8), located about 38 n.mi. southwest of Midway Islands, an extensive survey of the seamount was conducted between June and November 1980 on the *Townsend Cromwell*. The preliminary smooth-plot boat sheets prepared from the unprocessed and unverified depth data indicated that the shallowest area on Nero Seamount was about 62 m.

Seamount 8, a relatively small seamount about 64 m deep at its shallowest point, is located about 40 n.mi. northwest of Lisianski Island. Seamount 9 is actually a sea peak or pinnacle with a

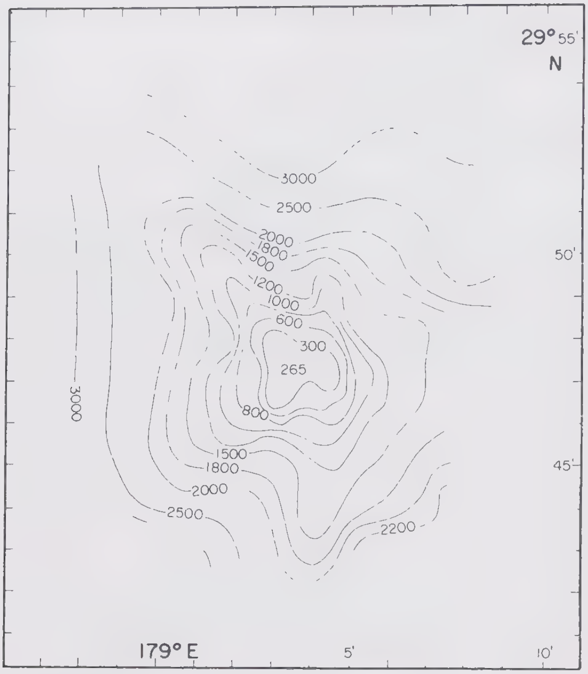

29° 55'
N
3000
2500
2000
1800
1500
1200
1000
600
300
265
800
1500
1800
2000
2500
2200
3000
50'
45'
179° E
5'
10'

Figure 6.—Bathymetry (m) of the northwest peak of SE Hancock Seamount (from Japan Fisheries Agency, 1974).

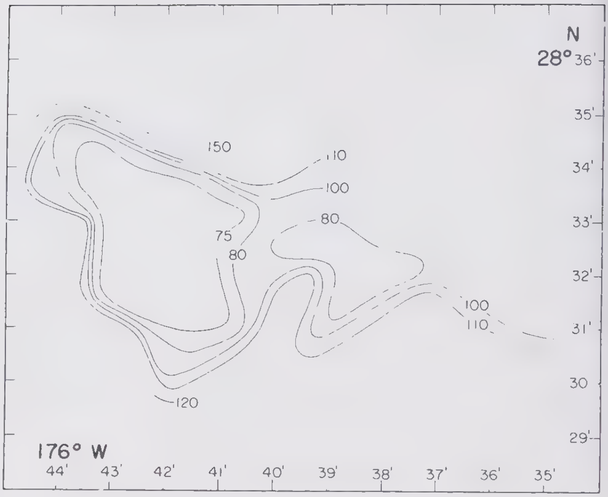
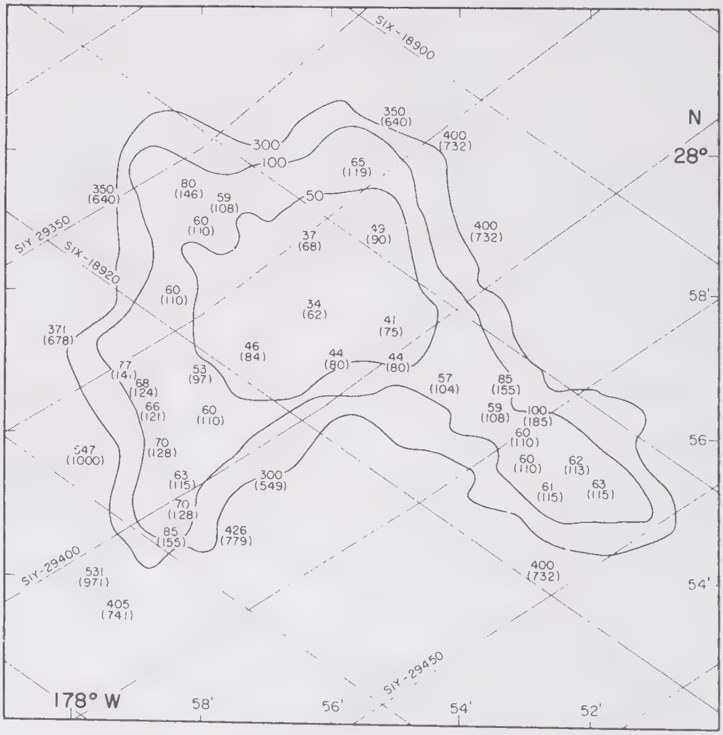

N
28° 36'
35'
34'
33'
32'
31'
30
29'
150
110
100
80
75
80
100
110
120
176° W
44'
43'
42'
41'
40'
39'
38'
37'
36'
35'

Figure 7.—Bathymetry (m) of Ladd Seamount (from Japan Fisheries Agency, 1974).

Figure 8.—Uncorrected bathymetry in fathoms (number in parentheses denotes meters) of Nero Seamount. Bathymetric chart prepared from soundings made during a hydrographic survey of the seamount by the *Townsend Cromwell* in June-November 1980.


SIX-18900
SIY 29350
SIX-18920
SIY-29400
SIY-29450
350 (640)
400 (732)
300
100
50
65 (119)
350 (640)
80 (146)
59 (108)
60 (110)
37 (68)
49 (90)
400 (732)
60 (110)
34 (62)
41 (75)
371 (678)
46 (84)
44 (80)
44 (80)
77 (141)
68 (124)
53 (97)
57 (104)
85 (155)
66 (121)
60 (110)
59 (108)
100 (185)
60 (110)
547 (1000)
70 (128)
60 (110)
62 (113)
63 (115)
300 (549)
61 (115)
63 (115)
70 (128)
85 (155)
426 (779)
531 (971)
400 (732)
405 (741)
N
28°
58'
56'
54'
178° W
58'
56'
54'
52'

recorded depth of 115 m. About 40 n.mi. northwest of Kure is Seamount 10 which has a reported depth of 329 m. Seamount 11, located 135 n.mi. southeast of Hancock, is reported to average less than 180 m deep. The eastern edge of this seamount is steep, whereas the western side is gently sloped. The summit is very rough.

Sampling Gear

Our primary sampling tool was the bottom trawl operated in an exploratory mode to determine the distribution and composition of the seamount community. Before deploying the trawl at each seamount, acoustic soundings were made to determine its topographic profile. After mapping, the trawl was deployed on the basis of seabed conditions.

Trawling was conducted initially with an 80 percent scale, high-opening Norwegian fish trawl with a 20 m headrope, 25 m footrope, 3.8 cm mesh codend cover, and equipped with 36 cm diameter rollers. In mid-1977, this was replaced with a Noreastern otter trawl

Table 5.—Fishes caught on the *Townsend Cromwell* by trawling over Hancock and other seamounts. The species are listed in descending order of their abundance (total catch) in weight.

Scientific name	Family	No.	Weight (kg)	Scientific name	Family	No.	Weight (kg)
Pentaceros richardsoni	Pentacerotidae	11,546	5,277				
Promethichthys prometheus	Gempylidae	282	172	*Beryx* sp.	Berycidae	1	<1
Beryx splendens	Berycidae	893	147	*Symphysanodon typus*	Lutjanidae	1	<1
Zenopsis nebulosa	Zeidae	269	94	*Parabothus* sp.	Bothidae	1	<1
Squalus blainvillei	Squalidae	61	67	*Laemonema rhodochir*	Moridae	3	<1
Cookeolus boops	Priacanthidae	42	36	*Polymixia* sp.	Polymixiidae	1	<1
Ariomma lurida	Nomeidae	184	29	*Argentina* sp.	Argentinidae	36	<1
Caprodon schlegelii	Serranidae	34	19	*Physiculus* sp.	Moridae	24	<1
Antigonia steindachneri	Antigoniidae	105	5	*Lophiomus miacanthus*	Lophiidae	3	<1
Polymixia japonica	Polymixiidae	35	4	*Isistius brasiliensis*	Squalidae	4	<1
Etmopterus pusillus	Squalidae	6	4	*Symphysanodon maunaloae*	Lutjanidae	5	<1
Antigonia eos	Antigoniidae	124	3.34		Sternoptychidae	11	<1
Ruvettus pretiosus	Gempylidae	1	3.30	*Beryx decadactylus*	Berycidae	1	<1
Macrorhamphosus sp.	Macrorhamphosidae	20	2.78	*Hoplichthys* sp.	Hoplichthyidae	1	<1
Diaphus trachops	Myctophidae	145	2.60	*Plectranthias kelloggi*	Serranidae	5	<1
	Brotulidae	36	2.54	*Astronesthus lucifer*	Astronesthidae	1	<1
Emmelichthys sp.	Emmelichthyidae	17	2.50	*Argyropelecus aculeatus*	Sternoptychidae	2	<1
Chromis struhsakeri	Pomacentridae	19	1.82	*Physiculus grinnelli*	Moridae	1	<1
Physiculus edelmanni	Moridae	18	1.69	*Argyripnus atlanticus*	Gonostomatidae	1	<1
Hyperoglyphe japonica	Nomeidae	7	1.44	*Parapercis roseoviridis*	Parapercidae	2	<1
Conger sp.	Congridae	11	<1	*Peristedion engyceros*	Peristediidae	1	<1
Chascanopsetta prorigera	Bothidae	5	<1	*Antigonia* sp.	Antigoniidae	8	<1
					Gonostomatidae	1	<1
Rhynchocymba nystromi nystromi	Congridae	4	<1	*Callanthias* sp.	Serranidae	9	<1
	Gempylidae	1	<1		Zeidae	14	<1
Parabothus coarctatus	Bothidae	2	<1		Lophotidae	1	<1
Peristedion sp.	Triglidae	1	<1		Muraenidae	1	<1
	Bothidae	11	<1	*Symphysanodon* sp.	Lutjanidae	2	<1
				Parapercis multifaciata	Parapercidae	1	<1

(Gunderson and Sample, 1980) which was larger than the Norwegian trawl, having headrope and footrope lengths of 27 and 32 m, respectively, 3.2 cm mesh cod-end liner, and rubber bobbins with diameters of 36 and 46 cm. Doors used to spread the two types of trawls were 1.8 × 2.7 m steel V-type, each weighing about 454 kg. A net sonde was attached to the center of the headrope to monitor the depth of fishing.

Day and night tows at an average speed of 2-3 knots were made at each trawl station. Trawling time varied from 5 to 38 minutes but was usually between 15 and 25 minutes depending on the extent of the trawlable area over the seamount. Catches were sorted by species, counted, and weighed. Large catches were subsampled to obtain estimates of the total catch. Biological collections were made for age, growth, and feeding studies.

In addition to the trawl, we used handlines, fish traps, and lobster pots to sample species that would not be caught in a trawl or in areas where trawling was not practical due to the rough summits of some of the seamounts. Handlines, operated with hydraulic gurdies, were fitted with either short terminal rigs of 4-6 incurved hooks (No. 18-32) or long droplines of 20 incurved hooks (No. 16-18). Bait was cut fish or squid. Fish traps, either single or in strings of up to four, measured 1.5 × 0.9 × 0.6 m; the reinforcing steel frame was covered with 2.5 cm square galvanized welded wire mesh. The two types of lobster pots used were the large-mesh pot measuring 0.9 × 0.6 × 0.4 m and covered with 5.1 × 10.2 cm heavy-duty, galvanized wire mesh, and the small-mesh pot measuring 1.1 × 0.8 × 0.5 m and covered with 1.2 × 2.5 cm hardware cloth. Traps and pots, baited with mackerel, had identical conical entrances with outer and inner diameters of 30.0 and 16.5 cm, respectively.

Trawling

The *Townsend Cromwell* trawled over the seamounts during 6 cruises, making 12 hauls at NW Hancock, 7 at SE Hancock, and 1 each at Seamounts 10 and 11[6]. All remaining seamounts, including Ladd and Nero and Seamounts 8 and 9, were sampled with other gear owing either to the roughness or very limited extent of the summit.

We noted a variation in catches and progressively better catches on later cruises. Although most of the trawl hauls were made when the echo sounder showed "fish signs" near the bottom, a few midwater hauls were made when the sounder indicated fish schools at middepths, but these hauls were invariably unproductive. Furthermore, because near-bottom trawling over the seamounts was a new operation for the ship's officers, crew, and Honolulu Laboratory scientists, we needed sufficient opportunity to become familiar with the net in the limited time available on each cruise. Therefore, catches made prior to 1979 (*Townsend Cromwell* cruises 76-06, 77-02, and 78-03) may have been greatly influenced by lack of experience and other factors.

The trawl catches, composed of 47 fish species representing 30 families (Table 5), included a diverse variety of species of commercial and noncommercial value. By far the most important was the pelagic armorhead, followed by the snake mackerel, *Promethichthys pro-*

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[6] Unlike the Japanese commercial trawlers, the *Townsend Cromwell*'s trawl haul represents only bottom time of the net; therefore, trawling time is not comparable with that of the Japanese trawlers.

Table 6.—Trawl station data and catches of predominant species at Hancock and other seamounts, 1976-81.

Seamount	Cruise	Date	Gear	Time started	Trawling time (min.)	Depth of tow (m)	Distance trawled (km)	Surface temp. (°C)	Bottom temp (°C)	Catch (kg) Pelagic armorhead	Alfonsin	Mirror dory	Snake mackerel	Horny dogfish	Others	Total	Total catch per hour (kg)	Pelagic armorhead in catch (%)
NW Hancock	78-03	9/8/78	Noreastern	2010	5	283-302	0.6			0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0
NW Hancock	78-03	9/9/78	Noreastern	1324	10	285-302	0.9	26.6	12.0	0.0	0.1	3.2	0.0	0.0	1.0	3.3	19.8	0.0
NW Hancock	78-03	9/9/78	Noreastern	2150	15	283-302	1.3	26.6	12.0	69.5	5.7	23.8	25.4	0.0	16.3	140.7	562.8	49.4
NW Hancock	78-03	10/9/78	Noreastern	0925	23	283-302	2.2	26.6	12.0	11.2	0.0	6.9	0.0	0.0	0.6	18.7	48.8	59.9
NW Hancock	78-03	10/9/78	Noreastern	1115	20	283-302	1.8	26.6	12.0	9.2	18.1	9.9	0.0	0.0	1.0	37.2	111.6	24.7
NW Hancock	79-02	5/4/79	Noreastern	1458	14	269-272	1.3	19.9	15.0	9.8	0.0	0.5	0.0	0.0	0.8	11.1	47.6	88.3
NW Hancock	79-02	5/5/79	Noreastern	1000	17	263-366	1.5	20.9	14.9	3.5	0.0	2.8	0.0	0.0	0.5	6.8	24.0	51.5
NW Hancock	79-02	5/5/79	Noreastern	2116	11	263-293	1.1	20.4	14.2	93.7	4.7	1.0	10.5	0.0	4.1	114.0	621.8	82.2
NW Hancock	79-02	5/5/79	Noreastern	2320	13	258	1.1	20.5	14.9	207.5	1.4	1.4	7.0	8.5	2.4	228.2	1,053.2	90.9
NW Hancock	79-02	5/6/79	Noreastern	0155	12	263	1.1	20.5	14.4	25.1	7.8	4.7	128.2	0.0	0.0	165.8	829.0	15.1
NW Hancock	80-02	4/17/80	Noreastern	1647	11	260	1.1	19.8		[1]4.2	[1]0.2	[1]2.1	0.0	0.0	0.0	6.5	35.4	64.6
NW Hancock	80-02	4/17/80	Noreastern	1934	18	260	1.7	19.7		1,308.8	51.1	4.6	0.0	9.5	2.1	1,376.1	4,587.0	95.1
Total					169					1,742.5	89.1	60.9	171.1	18.0	26.8	2,108.4		
Average catch per hour										618.6	31.6	21.6	60.7	6.4	9.5		748.5	82.6
SE Hancock	76-06	10/29/76	Norwegian	2133	19	265-293	1.8	25.2	13.5	20.9	0.4	0.0	0.0	0.0	4.1	25.4	80.2	82.3
SE Hancock	77-02	5/25/77	Noreastern	2200	20	269-530	1.8			0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0
SE Hancock	77-02	5/26/77	Noreastern	0848	20	263-311	1.8	21.5	12.6	20.0	0.6	3.6	0.0	0.0	[2]41.9	66.1	198.3	30.2
SE Hancock	79-02	5/6/79	Noreastern	2100	38	256	3.5	19.9	14.8	545.9	7.4	6.8	1.1	43.5	10.8	615.5	971.8	88.7
SE Hancock	80-02	4/16/80	Noreastern	1555	25	258	2.2	20.1		15.4	0.0	14.7	0.0	0.4	0.0	30.5	73.2	50.5
SE Hancock	80-02	4/16/80	Noreastern	2157	23	258	2.2	20.0		1,332.8	44.4	7.4	0.0	0.0	0.0	1,384.6	3,612.0	96.2
SE Hancock	81-02	3/31/81	Noreastern	2230	21		1.8	20.0		1,599.1	4.8	0.6	0.0	3.4	0.5	1,608.4	4,595.4	99.4
Total					166					3,534.1	57.6	33.1	1.1	47.3	57.3	3,730.5		
Average catch per hour										1,277.4	20.8	12.0	0.4	17.1	20.7		1,348.4	94.7
Seamount 11	78-01	2/12/78	Noreastern	1305	12	188-207	0.9	17.2		0.0	0.0	0.0	0.0	0.0	[1]1.0	[1]1.0	0.0	0.0
Seamount 10	76-06	10/30/76	Norwegian	2306	30	164-170	2.8	25.1	15.3	0.0	0.0	0.0	0.0	2.0	[3]59.2	61.2	122.4	0.0

[1] Estimated from average weights

[2] Predominantly driftfish, *Ariomma lurida*.

[3] Predominantly red bigeye, *Cookeolus boops*, and a grouper, *Caprodon schlegelii*.

metheus; alfonsin; mirror dory, *Zenopsis nebulosa*; and horny dogfish, *Squalus blainvillei*. The duration of the trawl hauls at NW Hancock ranged from 5 to 23 minutes/haul and averaged 14.1 minutes for a total of 2.8 hours of trawling (Table 6). The 12 hauls produced 1,742 kg of pelagic armorhead and 89 kg of alfonsin, or a ratio of 19:1. The CPUE varied from <1 to 4,587 kg/hour and averaged 748 kg/hour. Of the 12 hauls made at NW Hancock, only one produced a fairly large catch (1,309 kg) of pelagic armorhead. The remaining hauls produced 208 kg or less. The percentage of pelagic armorhead in the catch varied widely from 15 to 95 percent and averaged 83 percent.

The average catch rate at SE Hancock was higher than that at NW Hancock; however, monitoring of both seamounts will be required before definitive conclusions can be drawn about the stock. Trawling time per haul at SE Hancock ranged from 19 to 38 minutes, averaged 23.7 minutes/haul, and totaled 2.8 hours over seven trawl stations. The total catch included 3,534 kg of pelagic armorhead and 58 kg of alfonsin, or a ratio of 49:1. The CPUE varied from <1 to 4,595 kg/hour and averaged 1,348 kg/hour. Pelagic armorhead constituted between 30 and 99 percent of the catch.

At Seamount 10, the catch was practically nil in a 12-minute haul. A single haul at Seamount 11 with the Norwegian trawl produced only small numbers of red bigeye, *Cookeolus boops*, and grouper, *Caprodon schlegelii*. Both seamounts, however, require considerable additional sampling before reliable estimates can be made of the resources.

Handlining

Results from handline fishing indicated that the trawl catches were not representative of the seamount community. Handline fishing stations were occupied nine times each at NW and SE Hancock Seamounts, four times at Seamount 11, seven times at Ladd Seamount, and twice each at Nero Seamount, Seamount 9, and Seamount 8; the catches included 25 fish species representing 15 families (Table 7, 8). Of the 15 families sampled, 10 were also rep-

Table 7.—Fishes caught on the *Townsend Cromwell* by handlining on Hancock and other seamounts. The species are listed in descending order of their abundance (total catch) in weight.

Scientific name	Family	No.	Weight (kg)
Etelis carbunculus	Lutjanidae	170	363.06
Epinephelus quernus	Serranidae	36	359.64
Pentaceros richardsoni	Pentacerotidae	343	149.78
Hyperoglyphe japonica	Nomeidae	23	66.45
Scomber japonicus	Scombridae	46	65.93
Seriola dumerili	Carangidae	7	64.82
Squalus blainvillei	Squalidae	53	62.85
Caranx ignobilis	Carangidae	1	28.70
Cookeolus boops	Priacanthidae	9	19.40
Etelis coruscans	Lutjanidae	2	16.69
Pristipomoides zonatus	Lutjanidae	11	16.52
Decapterus tabl	Carangidae	12	13.28
Promethichthys prometheus	Gempylidae	13	12.04
Pontinus macrocephalus	Scorpaenidae	9	11.11
Beryx splendens	Berycidae	13	11.09
Pristipomoides sieboldii	Lutjanidae	8	6.95
Pseudocaranx dentex	Carangidae	1	5.20
Seriola aureovittata	Carangidae	1	5.00
Bodianus oxycephalus	Labridae	2	2.50
Decapterus sp.	Carangidae	1	1.25
Polymixia japonica	Polymixiidae	2	0.80
	Emmelichthyidae	1	0.73
Plectranthias kelloggi	Serranidae	2	0.60
Anthias bicolor	Serranidae	1	0.20
Sphoeroides cutaneous	Tetraodontidae	1	

resented in the trawl catches. In terms of species, however, only eight were also sampled by the trawl. Most of the remaining 17 species (including one unidentified species) were from the families Carangidae and Lutjanidae; members of the families Scombridae, Scorpaenidae, Labridae, and Tetraodontidae contributed most of the remainder.

Although handline fishing is selective in that the bait used, depth fished, hook size, and bottom type influence the species composition of the catch, the catch results were particularly valuable in providing information on fish distribution. Going from northwest to southeast, we found the Hancock Seamounts' handline catches dominated by pelagic armorhead; alfonsin; butterfish, *Hyperoglyphe japonica*; chub mackerel, *Scomber japonicus*; mackerel scad, *Decapterus tabl*; two groupers, *Plectranthias kelloggi* and *Anthias bicolor*; and horny dogfish. At Seamount 11, catches of horny dogfish predominated; however, members of the tropical snapper-grouper complex were also more in evidence (Table 8). At Ladd and Nero Seamounts, members of the pelagic armorhead-alfonsin complex were almost completely absent, whereas fishes of the snapper-grouper complex such as red snapper, *Etelis carbunculus* (formerly *E. marshi*); grouper, *Epinephelus quernus*; amberjack, *Seriola dumerili*; Brigham's snapper, *Pristipomoides zonatus*; and pink snapper, *P. sieboldii*; were prominent in the catches.

Our results corroborated those of Japanese investigators who found that the pelagic armorhead-alfonsin complex over the summits of the central North Pacific seamounts gave way to a fish community dominated by tropical species in areas with warmer waters and over those seamounts to the east of the 180th meridian (Japan Marine Fishery Resource Research Center, 1973; Japan Fisheries Agency, 1974; Sasaki, 1974, 1978).

Table 8.—Number of fish caught by handline at the various seamounts and arranged by families in their phyletic order (weight in kilograms in parentheses).

Family and species	NW Hancock	SE Hancock	Seamount 11	Ladd	Nero	Seamount 9	Seamount 8
Squalidae							
Squalus blainvillei	8 (14.17)	34 (42.96)	10 (1.56)	1 (4.16)	—	—	—
Polymixiidae							
Polymixia japonica	—	—	—	<1	2 (0.80)	—	—
Berycidae							
Beryx splendens	11 (9.55)	2 (1.54)	—	<1	—	-	—
Scorpaenidae							
Pontinus macrocephalus	—	—	—	5 (6.22)	3 (3.50)	1 (1.39)	—
Serranidae							
Epinephelus quernus	—	—	4 (36.92)	8 (92.32)	10 (73.50)	6 (72.51)	8 (84.39)
Anthias bicolor	1 (0.20)	—	—	<1	—	—	—
Plectranthias kelloggi	1 (0.40)	1 (0.20)	–	1	—	—	—
Priacanthidae							
Cookeolus boops	—	—	4 (6.80)	2 (5.20)	3 (7.40)	—	—
Carangidae							
Pseudocaranx dentex	—	—	—	1	1 (5.20)		–
Caranx ignobilis	—		—	—	—	—	1 (28.70)
Decapterus sp.	—	—		1 (1.25)	—	—	—
D. tabl	1 (1.25)	11 (12.03)	—	1	—	—	—
Seriola aureovittata	—	—		1 (5.00)		–	–
S. dumerili	—	—	—	1	—	1 (9.57)	6 (55.25)
Lutjanidae							
Etelis carbunculus	—	—	–	55 (126.39)	77 (153.90)	7 (10.11)	31 (72.66)
E. coruscans	—	–	—	2 (16.69)	—	—	—
Pristipomoides sieboldii	—	—	—	5 (5.31)	1 (0.70)	2 (0.94)	—
P. zonatus	—	—	—	<1	—	1 (2.08)	10 (14.44)
Emmelichthyidae	—	—	—	<1	—	1 (0.73)	—
Pentacerotidae							
Pentaceros richardsoni	188 (85.67)	154 (62.11)	—	1 (2.00)		-	
Labridae							
Bodianus oxycephalus	—	—	—	<1	2 (2.50)	—	—
Gempylidae							
Promethichthys prometheus	—	—	—	12 (11.24)	1 (0.80)	—	—
Scombridae							
Scomber japonicus	2 (2.56)	44 (63.37)	—	<1			
Nomeidae							
Hyperoglyphe japonica	15 (29.75)	7 (27.70)	—	1 (9.00)	—	—	—
Tetraodontidae							
Sphoeroides cutaneous	—	—	—	1 (<1)	-	—	—

Table 9.—Fishes and invertebrates caught on the *Townsend Cromwell* by trap on Hancock and other seamounts. The species are listed in descending order of their abundance (total catch) in weight.

Scientific name	Family	No.	Weight (kg)
Squalus blainvillei	Squalidae	134	148.41
Epinephelus quernus	Serranidae	15	91.64
Seriola dumerili	Carangidae	3	27.00
Pristipomoides filamentosus	Lutjanidae	5	19.91
Pseudocaranx dentex	Carangidae	3	12.49
Polypus sp.	Polypodidae	4	10.27
Gymnothorax steindachneri	Muraenidae	9	7.50
Etelis carbunculus	Lutjanidae	2	5.22
Physiculus grinnelli	Moridae	19	5.03
Gymnothorax sp.	Muraenidae	3	4.19
	Congridae	2	3.73
Ariosoma bowersi	Congridae	1	2.40
Scyllarides squammosus	Scyllaridae	1	1.38
	Moridae	7	1.34
Conger wilsoni	Congridae	1	1.27
	Muraenidae	1	1.15
Pentaceros richardsoni	Pentacerotidae	2	1.01
Plectranthias kelloggi	Serranidae	4	0.80
Gymnothorax berndti	Muraenidae	1	0.77
Congrellus aequoreus	Congridae	2	0.68
Coris ballieui	Labridae	5	0.58
Antigonia steindachneri	Antigoniidae	2	0.20
Etmopterus villosus	Squalidae	1	0.10
Antigonia eos	Antigoniidae	2	0.06
Parapercis multifasciata	Parapercidae	1	—
Squalus sp.	Squalidae	1	—
Gymnothorax undulatus	Muraenidae	1	—
	Bramidae	2	—
Chaetodon miliaris	Chaetodontidae	2	—
Chaetodon fremblii	Chaetodontidae	1	—
Lupocyclus quinquedentatus	Portunidae	1	—
	Astropectinidae	16	—
	Paguridae	81	—
	Echinometridae	8	—
Calappa sp.	Calappidae	2	—
	Gastropoda	2	—

Table 10.—Number of fish caught by fish and lobster traps at various seamounts and arranged by families in phyletic order (weight in kilograms in parentheses, when available).

Family and species	NW Hancock	SE Hancock	Seamount 11	Nero	Ladd	Seamount 8
Astropectinidae			1	5	10	—
Echinometridae			—	8	—	—
Gastropoda (Class)	—	—	—	—	2	—
Polypodidae						
Polypus sp.	—	—	—	—	[1]— (10.27)	—
Scyllaridae						
Scyllarides squammosus	—	—	—	—	—	1 (1 38)
Paguridae						
Dardanus spp.	—	—	—	31	38	12
Calappidae						
Calappa sp.	—	—	—	—	—	2
Portunidae						
Lupocyclus quinquedentatus	—	—	—	—	1	—
Squalidae						
Etmopterus villosus	—	1 (0.10)	—	—	—	—
Squalus sp.	—	1	—	—	—	—
Squalus blainvillei	7 ([2]8.26)	120 (121.63)	6 (13 27)	1 (5.25)	—	—
Muraenidae						
Gymnothorax sp.	—	—	3 (4 19)	—	—	—
G. berndti	—	—	—	—	1 (0.77)	—
G. steindachneri	—	—	—	2 ([3]1.88)	7 (5.62)	—
G. undulatus	—	—	—	1	—	—
Moray (unidentified)	—	—	—	—	1 (1.15)	—
Congridae						
Ariosoma bowersi	—	—	—	—	1 (2.40)	—
Conger wilsoni	—	—	1 (1.27)	—	—	—
Congrellus aequoreus	—	—	—	—	2 (0.68)	—
Conger eels (unidentified)	—	—	—	—	2 (3.73)	—
Moridae						
Physiculus grinnelli	—	—	—	6 (1.70)	13 (3.33)	—
Morid fishes	—	1 (0.17)	6 (1.17)	—	—	—
Antigoniidae						
Antigonia eos	1 ([2]0.03)	1 (0.03)	—	—	—	—
A. steindachneri	2 ([1]0.20)	—	—	—	—	—
Serranidae						
Epinephelus quernus	—	—	7 (33.04)	—	8 (58.60)	—
Plectranthias kelloggi	4 ([2]0.80)	—	—	—	—	—
Carangidae						
Pseudocaranx dentex	—	—	—	—	3 (12.49)	—
Seriola dumerili	—	—	—	3 (27.00)	—	—
Lutjanidae						
Etelis carbunculus	—	—	—	—	2 (5.22)	—
Pristipomoides filamentosus	—	—	—	2 (12.01)	—	3 (7 90)
Bramidae	—	—	—	—	2	—
Chaetodontidae						
Chaetodon fremblii	—	—	—	—	—	1
C. miliaris	—	—	—	—	1	1
Pentacerotidae						
Pentaceros richardsoni	—	2 (1.01)	—	—	—	—
Labridae						
Coris ballieui	—	—	—	—	4 (0.46)	1 ([3]0 12)
Parapercidae						
Parapercis multifasciata	1	—	—	—	—	—

[1] Number caught not recorded; estimated to be fewer than seven animals.
[2] Estimated from average weight of handline and trawl-caught specimens
[3] Estimated from average weight of trap-caught specimens.

Trapping

The fishes and invertebrates caught in the fish traps and lobster pots on the six cruises are presented in Table 9. Of primary interest is that only two pelagic armorhead and no alfonsin were caught in 60 trap-nights and 176 pot-nights of effort expended. It was suggested that pelagic armorhead and alfonsin do not feed in the area immediately adjacent to the summits and, therefore, are not vulnerable to traps. Examination of our handline catches, however, showed that they were usually taken on hooks fishing closest to the bottom. This indicated that although these species feed near the bottom, they cannot be trapped readily.

Representatives of 13 fish families including 24 species were caught in the traps (Table 10); the horny dogfish was the dominant species in the catches. Of the 13 families, 9 were also represented in the trawl catch; however, 15 of the positively identified species were not present in the trawl catch. With the exception of pelagic armorhead and alfonsin, the handline catches differed from the trawl catches in that most of the other species in the handline catches included members of the snapper-grouper complex. The trap and pot catches, on the other hand, included large numbers of not only horny dogfish, snappers, groupers, and carangids, but also bottom-dwelling forms such as conger eels, including *Ariosoma bowersi*, *Conger wilksoni*, *Congrellus aequoreus*, and an unidentified species; and moray eels, including *Gymnothoras berndti*, *G. steindachneri*, *G. undulatus*, *Gymnothorax* sp., and an unidentified species; and invertebrates such as starfish, Astropectinidae; and hermit crabs, *Dardanus* spp. Other invertebrates caught in the traps and pots

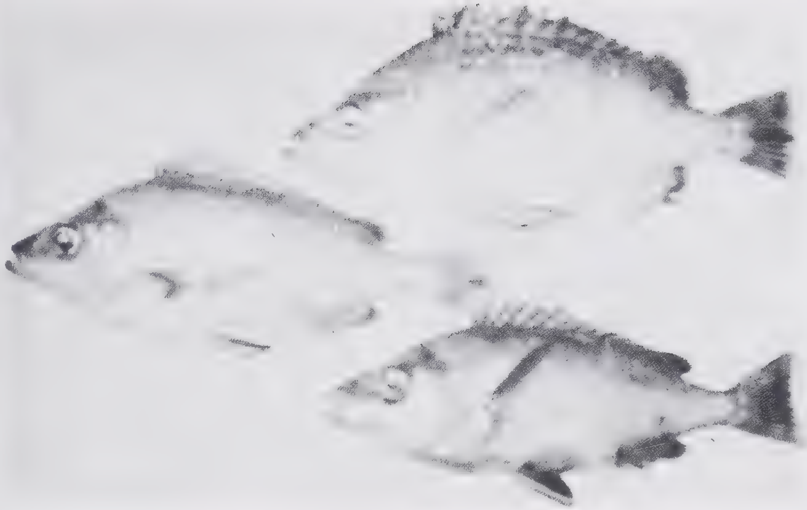

Figure 9.—Pelagic armorhead, *Pentaceros richardsoni*. Examples of "fat" (upper right), "intermediate" (center), and "lean" (lower right) fish, which are discussed in the section "Pelagic Armorhead."

included octopus, *Octopus* sp.; slipper lobster, *Scyllarides squammosus*; swimming crab, *Lypocyclus quinquedentatus*; box crab, *Calappa* sp.; sea urchin, Echinometridae; and unidentified gastropods.

Target Species' Biology

Pelagic Armorhead

Formerly considered a rare species because of the paucity of reports on its capture, the pelagic armorhead (Fig. 9), in the family Pentacerotidae, is broadly distributed in the North Pacific between lat. 30° and 50°N (Takahashi and Sasaki, 1977). The outstanding feature of members of this family is the unusual armature of the head, which is almost completely enclosed in exposed, rough, striated bones (Smith, 1964).

Very little is known about the life history of this species. Eggs and larvae are thought to be free-floating and dispersed by waters of the North Equatorial Current (Chikuni, 1971b). It has also been hypothesized that the juveniles remain pelagic until age 4-5 (25-30 cm fork length) when they begin a demersal existence over the seamounts.

In addition to the Pacific seamounts we have discussed, pelagic armorhead have been recorded from New Zealand, Australia, the northern part of the Hawaiian Archipelago, Japan, Gulf of Alaska, British Columbia, Oregon, and California (Abe, 1957; Clemens and Wilby, 1961; Wagner and Bond, 1961; Follett and Dempster, 1963; Honma and Mizusawa, 1969).

Not all seamounts in the North Pacific have populations of pelagic armorhead. Trawling surveys over Patton (lat. 54°40′N, long. 150°30′W) and Cobb Seamounts (lat. 46°46′N, long. 130°49′W) in the northeastern Pacific have not demonstrated the presence of pelagic armorhead (Chikuni, 1971a, b). Seamounts north of lat. 35°N in the Emperor Chain have summits so deep that the possibility of finding pelagic armorhead on them appears rather remote. Furthermore, those seamounts located on the Hawaiian Ridge to the east of the 180th meridian are relatively shallow and trawling surveys have demonstrated that their fauna is subtropical and do not include the pelagic armorhead (Sasaki, 1978).

Pelagic armorhead also make extensive vertical migrations, depending on the location in the North Pacific. Japanese trawlers have fished for pelagic armorhead in depths varying from 300 to 600 m over the central North Pacific seamounts. However, unlike other mesopelagic species that ascend into the surface layers at night and descend to great depths during the day, pelagic armorhead have been found close to the top of the seamounts at night in most instances. Furthermore, reports of their capture by handlines suggested that the pelagic armorhead may also be schooling at the surface at night (Chikuni, 1970).

Other reports suggest that pelagic armorhead do not confine their vertical migration to the water mass overlying the tops of the seamounts. Observations by Kitani and Iguchi (1974) showed that they rise above and descend below the top of the seamount during the day and night, respectively. The catch per unit of effort by trawling usually peaked between 0300 and 0700 hours and between 1700 and 1900 hours. Therefore, the pelagic armorhead appear to migrate through the level of the seamount summit twice a day—once in the morning and again in the evening.

Studies on feeding behavior support the contention that pelagic armorhead feed at night near the surface. Observations on aquarium-held fish indicate that pelagic armorhead in their natural environment probably feed at night on organisms occurring near the surface (Hart, 1973). Stomach contents of pelagic armorhead caught over the seamounts contained euphausids, mysids, copepods, salps, shrimps, myctophids, and other organisms usually associated with the deep-scattering layer (Sasaki, 1973, 1974). Since the deep-scattering layer ascends toward the surface at night and remains deeper during daylight, the results of the stomach analysis tend to agree with aquarium observations.

The fork lengths of unsexed pelagic armorhead caught by trawling showed strong unimodal distributions. At NW Hancock, the fish ranged from 23.3 to 39.8 cm (average 29.7 cm) and 67 percent were between 29 and 31 cm (Fig. 10). The fish from SE Hancock showed a similar narrow length range of 23.3-35.9 cm and averaged 29.9 cm, which was nearly identical to that found for NE Hancock (Fig. 11). Here about 62 percent of the fish fell within the 29-31 cm length range. An analysis of variance showed that mean size at NW Hancock was not significantly different from that at SE Hancock ($F = 1.65$; df = 1 and 553; $P > 0.05$). Males, however, differed significantly in size from females (Table 11). The average size of females was from 0.8 to 1.4 cm larger than that of the males.

One of the more perplexing problems in the life history of the pelagic armorhead is the morphological differences of fish over the various seamounts in the Pacific. Sasaki (1974) reported that the northeastern Pacific stock has a higher proportion of the "fat" type, whereas the central North Pacific stock has more "lean" fish. Coloration also differs. The "fat" type has a dark blue dorsal and white ventral regions which are typical of surface-dwelling fish. Some are also reticulated. The "lean" fish over the central North Pacific seamounts have been reported to be uniformly gray and without any markings.

On cruises of the *Townsend Cromwell* prior to 1980, as much as 95 percent of the pelagic armorhead caught at Hancock Seamounts were "lean." In 1980, however, about 20 percent of the fish at NW Hancock and about 15 percent at SE Hancock were "fat." By 1981 we found that proportion of "fat" to "lean" completely reversed from former years. From one trawl haul at SE Hancock, the catch included 94 percent "fat" and only 6 percent "lean." Furthermore, many of the "fat" fish could be classified into a third "intermediate" category and there actually was a gradation of body types from "very fat" to "very lean" (Fig. 9). This gradation of body types can also be seen in data collected by U.S. observers on the Japanese trawlers in 1980-81 (Table 12).

One explanation offered for the occurrence of "fat" and "lean" fish is that the body types are related to reproductive condition because a large number of the gonads of both sexes of "lean" fish were in the spent stage (Takahashi and Sasaki, 1977). This points to a possibility that the "lean" fish were unable to recover from the spawning ordeal. The "lean" fish, in many cases, showed signs of deterioration (i.e., the skin peeled off their bodies very readily (Kuroiwa, 1973)).

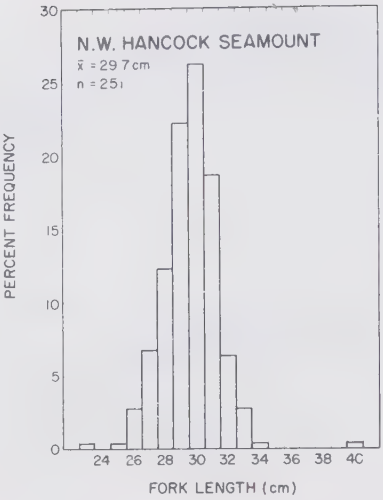

Figure 10.—Length-frequency distribution of pelagic armorhead caught at NW Hancock Seamount during *Townsend Cromwell* cruise 80-02.

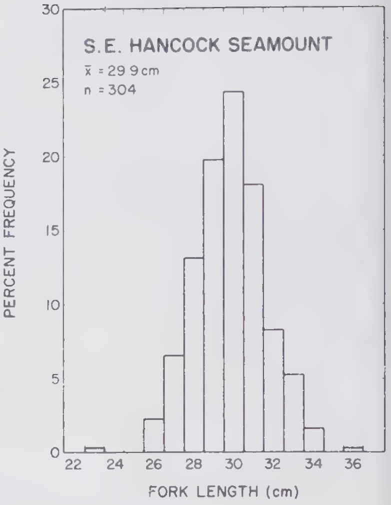

Figure 11.—Length-frequency distribution of pelagic armorhead caught at SE Hancock Seamount during *Townsend Cromwell* cruise 80-02.

Table 11.—Analysis of variance on the mean length of pelagic armorhead measured by sex, at NW and SE Hancock Seamounts.

		No. measured		Mean length (cm)			
Seamount	Cruise	Male	Female	Male	Female	Values of F	Probability
NW Hancock	78-03	23	46	29 6	30.7	7.70	0.01
	80-02	77	45	28.7	30.1	27.73	0.01
SE Hancock	78-01	19	53	29.0	30.1	17.19	0.01
	81-02	49	26	28.9	29.7	9.36	0.01

Table 12.—The percentage of "fat," "lean," and "intermediate" body types of pelagic armorhead in the catch of Japanese trawlers fishing at Hancock Seamounts in 1978-81.

			Percentage		
Vessel name	Date	Seamount	"Fat"	"Lean"	"Intermediate'
Ryuyo Maru No. 2	4/22- 6/ 3/78	Hancock	2	98	
Aso Maru	5/27- 7/10/79	Hancock	5	95	
Kitakami Maru	8/ 9-10/ 4/80	NW Hancock	27	73	
		SE Hancock	43	57	
Aso Maru	9/24- 9/30/80	NW Hancock	11	45	43
		SE Hancock	13	35	52
Aso Maru	6/ 9- 6/19/81	NW Hancock	60	25	15
		SE Hancock	59	24	17
Kitakami Maru	8/15-10/ 1/81	NW Hancock	67	33	
		SE Hancock	61	39	

Studies conducted by the Soviets and Japanese have demonstrated that spawning of pelagic armorhead begins in November-December, peaks in January-February, and declines in March (Iguchi, 1973; Sasaki, 1974; Takahashi and Sasaki, 1977). Therefore, one would expect the proportion of "lean" fish in the catch to be high during the post-spawning period. Data from our research cruises indicate otherwise. For example, from one trawl haul by the *Townsend Cromwell* at SE Hancock in March 1981, the catch was composed of 94 percent "fat" and 6 percent "lean" fish. If spawning peaked in January-February, then there should be a large proportion of "lean" fish in the catch in March. In addition, data from a Japanese trawler fishing from April through June 1978 indicated that "lean" fish represented 98 percent of the catch from Hancock, whereas on another trip from May through July 1979, 95 percent of the catch was "lean" (Table 12). It also appears that "fat" and "lean" fish are not segregated by depth because both body types are found in the same trawl haul. The inconsistency in these results points out the complexity of the pelagic armorhead's life history pattern and that additional studies are necessary to understand the changes in their morphological characteristics.

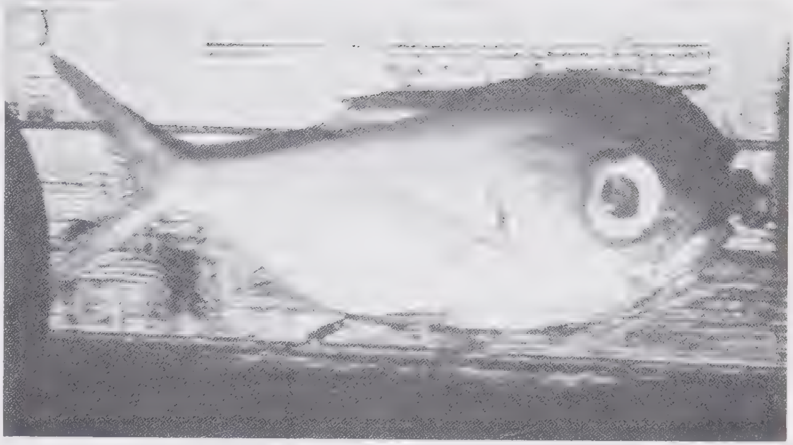

Figure 12.—Alfonsin, *Beryx splendens*.

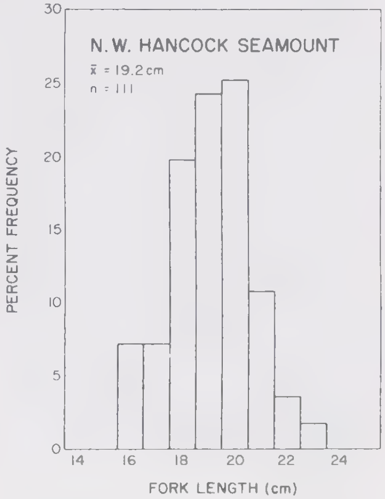

Figure 13.—Length-frequency distribution of alfonsin caught at NW Hancock Seamount on *Townsend Cromwell* cruise 80-02.

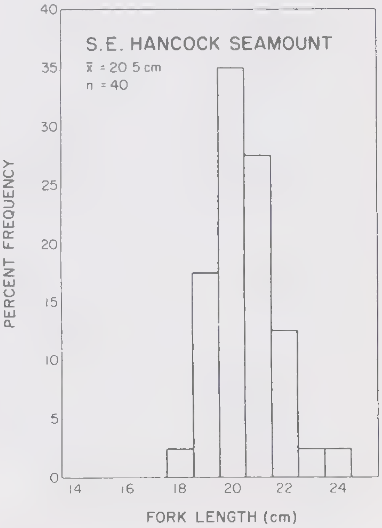

Figure 14.—Length-frequency distribution of alfonsin caught at SE Hancock Seamount on *Townsend Cromwell* cruise 80-02.

Alfonsin

The alfonsin (Fig. 12) which belongs to the Berycidae, a high-seas family of fishes, is bright red and inhabits rocky bottom several hundred meters deep. The species is found mainly in the western North Pacific where for many years it has been caught by handlines in Sagami Bay and Kashima Nada in the inshore areas of Japan and on the banks and slopes around Izu (South Honshu Ridge). In 1970, alfonsin were reported from Kinancho on the Kinan Seamount Range and the Kyushu-Palau Seamount Range. They also occur over the Emperor Seamounts where they were first taken by Soviet trawlers in November 1967 (Sakiura, 1972), and were caught by hook and line beginning in 1973 (Masuzawa et al., 1975). In the trawl fishery, alfonsin constitute only a small percentage of the catch.

A closely related species, *Beryx decadactylus*, has been taken in small numbers together with alfonsin. *Beryx decadactylus* has also been taken near Saipan in the Commonwealth of the Northern Mariana Islands with bottom gill nets.

Near Japan, alfonsin spawn between August and October and the eggs are transported by the Kuroshio (Chikuni, 1971b). Artificial propagation experiments showed that the berycoid eggs float and hatch in about 2 days at 23°C and newly hatched larvae float for 2-3 days before they begin to swim on the fourth day (Onishi, 1967). Therefore, the distribution of the larvae is wholly dependent on the Kuroshio and its offshoots.

Alfonsin migrate vertically during the evening to feed near the surface. Analysis of stomach contents of fish caught over the Emperor Seamount Chain disclosed that small fish predominated in 43 percent of the stomachs, whereas crustaceans (decapods, mysids, and euphausids) predominated in 37 percent of the samples. No information was available on the remaining 20 percent of the fish sampled (Aomori Prefectural Fisheries Experimental Station, 1976).

Figures 13 and 14 show the length-frequency distributions of unsexed alfonsin caught by trawl at NW and SE Hancock. Those caught at NW Hancock ranged from 15.7 to 23.0 cm and averaged 19.2 cm whereas those caught at SE Hancock had a narrower size range, from 18.2 to 23.7 cm, and averaged 20.5 cm. There was a highly significant difference in sizes of fish from the two seamounts ($F = 25.69$; df = 1 and 149; $P < 0.01$).

Summary and Conclusions

The seamount-groundfish trawl fishery expanded rapidly after 1967 when exploratory fishing by Soviet trawlers demonstrated the presence of commercial concentrations of pelagic armorhead and smaller quantities of alfonsin. In 1969, Japanese trawlers entered the fishery and their catches fluctuated widely until 1972, thereafter stabilizing at 18,952-34,538 t. Although the catch peaked in 1974, CPUE peaked much earlier, reaching 60.2/hour in 1972, then declined steadily to 9.7/hour by 1976. Unpublished Japanese data indicate that CPUE continued its downward trend in 1977-81, fluctuating between 0.3 and 2.4 t/hour.

During 1972-76, Hancock Seamounts, which fall within the U.S. FCZ around the Hawaiian Archipelago, received from 1 to 29 percent of the entire central North Pacific trawling effort by the Japanese. The catches during this period fluctuated from 653 to 8,518 t or roughly from 3 to 34 percent of the central North Pacific pelagic armorhead catch.

Based on catch data, the center of abundance of pelagic armorhead is near Colahan, C-H, and Hancock Seamounts, whereas that for alfonsin is in more northerly latitudes near Kimmei Seamount in the Emperor Seamount Chain.

In 1978-81, U.S. observers collected data on three Japanese trawlers that made six trips to Hancock Seamounts. These data indicated that after the intense fishing pressure applied prior to 1977, it had begun to improve and showed an upward trend although the CPUE was still considerably below the pre-1977 level.

Life history aspects of the pelagic armorhead are not well understood at present; however, much of the alfonsin's biology and ecology have been investigated by the Japanese.

Data collected by the *Townsend Cromwell* during research cruises to the seamounts in the Hawaiian Archipelago demonstrated that the species complex changes abruptly near Midway Islands. The pelagic armorhead-alfonsin complex predominated at Hancock Seamounts near the northern edge of the U.S. FCZ; however, slightly south of Hancock near Midway Islands and Kure Atoll, the snapper-grouper complex predominated at Ladd, Nero, and other unnamed seamounts in that area.

There was no significant difference in the mean length of pelagic armorhead from NW and SE Hancock. However, females were consistently larger than males. Significant differences in mean sizes were evident in alfonsin caught at NW and SE Hancock. One of the peculiarities noted among the pelagic armorhead population at Hancock Seamounts was the occurrence of "lean" and "fat" fish in the catch. Japanese investigators have hypothesized that body types are related to spawning with "lean" fish, the result of a postspawning condition. Research cruise data collected by the Honolulu Laboratory failed to substantiate this hypothesis. The manner in which apparent abundance (CPUE) of pelagic armorhead declined from its peak in 1972 while effort rose steadily from 1972 to 1976 and remained at relatively high levels in 1977-81 indicates that the trawl fishery has had a real effect on the stock. The failure of total catch to increase with increasing effort suggests that the rate of fishing has been sufficiently intense and may have surpassed the level corresponding to optimum fishing effort.

Although preliminary assessment studies have been attempted, reliable estimates are not possible until several critical problems are addressed. For example, there is a complete lack of catch and effort data from Soviet trawlers, no evidence that the stock and fishery dynamics over one seamount are independent of events occurring over other central Pacific seamounts, no information on what governs recruitment to the seamount habitat, and no logical explanation for the existence of "fat" and "lean" types on the same seamount. To solve these problems, we must promote not only careful assessment of the pelagic armorhead stock over its entire range, but also international management action, should it become necessary.

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LENGTH-WEIGHT AND STANDARD LENGTH-FORK LENGTH RELATIONSHIPS OF DEEPSEA HANDLINE FISHES OF THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Predictive and functional length-weight and standard length-fork (or total) length relationships were calculated from lengths and weights of eight major deepsea species caught by handline in the Northwestern Hawaiian Islands (NWHI). Data collected on RV *Townsend Cromwell* cruises from August 1978 to September 1981 were grouped by sex, cruise, and location of capture. Differences in slopes of regression lines between sexes, tested by ANCOVA for six species, were not significant. There were, however, significant differences among cruises for *Epinephelus quernus* and *Pristipomoides filamentosus*, the two most important species in the handline fishery. Among locations, differences in slopes were also not significant except for *E. quernus*. Pooling of data to calculate a single relationship representative of the whole population for each species, regardless of sex, cruise, or location of capture appeared justified. In this paper, length-weight relationships are given for eight major deepsea species caught by handline in the NWHI. These data represent conversion factors that should prove to be useful in the development of fishery management plans for the Hawaiian handline fishery.

bottomfish
length-weight
standard length-fork length
Northwestern Hawaiian Islands

INTRODUCTION

A deepsea handline fishery has been in existence in the Northwestern Hawaiian Islands since the mid-1940s. In 1976, the Magnuson Fishery Conservation and Management Act was enacted to extend U.S. jurisdiction over fishery resources out to 200 nautical miles from shoreline, and a management plan for the handline fishery resource in Hawaii was undertaken by the Western Pacific Regional Fishery Management Council. Between October 1976 and September 1981, the National Marine Fisheries Service (NMFS) conducted a series of resource survey and assessment cruises on the RV *Townsend Cromwell* and occasionally on a chartered commercial fishing vessel to collect data.

The catch of the deepsea handline fishery consisted primarily of eight species: greater amberjack, *Seriola dumerili*, pig ulua, *Pseudocaranx dentex* (= *Caranx cheilio*) (W.F. Smith-Vaniz, The Academy of Natural Sciences, 1981: personal communication), opakapaka, *Pristipomoides filamentosus* (= *P. microlepis*) (revised by Kami, 1973), kalekale, *P. sieboldii*, gindai, *P. zonatus* (= *Rooseveltia brighami*) (W.D. Anderson, College of Charleston, 1981: personal communication), ehu or ulaula, *Etelis carbunculus* (= *E. marshi*) (revised by Anderson, 1981), onaga, *E. coruscans* (= *E. carbunculus*) (revised by Anderson, 1981), and hapuupuu, *Epinephelus quernus*. These fishes were caught at the edge of banks between depths of 73 and 274 m.

There is no published life history information on any of these fishes from the NWHI and very little from elsewhere in the world. This report provides length-weight and standard length-fork length relationships of the eight major fish species caught on handline gear in the NWHI.

MATERIALS AND METHODS

Fork length (FL) or total length, standard length, weight, and sex were recorded for all fishes (Osteichthyes) caught at deepsea handline stations on the *Townsend Cromwell* survey cruises 78-03, 78-04, 79-02, 80-02, 80-03, 80-04, 80-05, 81-01, 81-02, 81-03, and 81-04 to the NWHI. Fork, total, and standard lengths were measured to the nearest millimeter with 1-m fish calipers according to Ricker (1980). Since the hapuupuu has a rounded tail, its total length was measured. The other fishes have forked tails. Although only fork length is mentioned in the balance of this manuscript, total length was used in place of fork length for hapuupuu. Weights were taken on a Maco (model 25) platform beam scale to the nearest 10 g. Prior to August 1978, weights were taken by spring scales and considered less accurate; these were not used in this study. Sex was determined by examining the gonads.

The length-weight data were examined for possible differences or changes due to sexual dimorphism, time of year (cruise), and area of capture (banks). For each species, the length-weight data were grouped by sex, cruise, and area of capture, and the slopes of the length-weight relationships for these groupings were compared by an analysis of covariance (ANCOVA) to test for equality of slopes among groups. When the group size was very small, <3, the data were not used. Computer program P1V from BMDP Statistical Software (Dixon, 1981) was used to perform the analyses. The decision to pool all data of the same species was made partially on the results of these tests. The relationship of weight to length is described by a power function of the form

$$W = aL^b$$

where

W = weight in kilograms
a = a constant (the Y-intercept)
L = fork length in millimeters
b = a constant (the regression coefficient or slope)

To fit a least square regression to the linear form of the length-weight power function, common log transformation of lengths and weights was required.

The predictive length-weight and standard length-fork length relationships were calculated by the BMDP computer program P6D (Dixon, 1981). The parameters for the functional length-weight, and standard length-fork length regression were calculated using the slopes of the predictive regression equations (Ricker, 1973).

RESULTS

Results of the ANCOVA comparing slopes and a tabulation of slopes for individual groups of six species of fish are listed by sex in Table 1, seven species by cruise in Table 2, and seven species by bank in Table 3. On the basis of these tests, all data were pooled for each species, so that single length-weight relationships would be representative of the whole NWHI population.

Parameters for the predictive and geometric mean (GM) functional length-weight regressions, sample size, correlation coefficients, and range of fork lengths for each species are tabulated in Table 4. Parameters for the predictive and GM functional standard length-fork length regressions are tabulated in Table 5. Functional length-weight curves for the eight deepsea fishes are illustrated in Figures 1 through 8.

TABLE 1. ANCOVA COMPARING EQUALITY OF SLOPES BETWEEN MALE AND FEMALE LENGTH-WEIGHT RELATIONSHIPS OF DEEPSEA HANDLINE FISHES

		Seriola dumerili	*Pseudocaranx dentex*	*Pristipomoides filamentosus*	*Pristipomoides sieboldii*	*Pristipomoides zonatus*	*Etelis carbunculus*
Males	Slope (b)	2.8539	2.9905	2.8340	3.1804	3.0732	2.9922
	Number (n)	106	128	194	27	34	238
Females	b	2.9577	2.9583	2.8727	3.0850	2.9657	3.0023
	n	71	132	240	89	45	496
All pooled	b	2.8986	2.9737	2.8584	3.1118	3.0121	2.9992
	n	177	260	434	116	79	734
	F value	1.7622	0.2621	1.6642	0.1295	0.2060	0.0326
	d.f.	1, 173	1, 256	1, 430	1, 112	1, 75	1, 730

TABLE 2. ANCOVA COMPARING EQUALITY OF SLOPES AMONG LENGTH-WEIGHT RELATIONSHIPS OF DEEPSEA FISHES GROUPED BY CRUISE

Cruise No.		*Seriola dumerili*	*Pseudocaranx dentex*	*Pristipomoides filamentosus*	*Pristipomoides sieboldii*	*Pristipomoides zonatus*	*Etelis carbunculus*	*Epinephelus quernus*
TC-78-03	Slope (b)	2.7759	2.9172	2.6880	2.4019	2.8394	2.9476	3.1833
	Number (n)	33	30	33	8	22	114	103
TC-78-04	b	2.9806	3.0941	2.7609	3.0276	—	2.3839	3.1245
	n	20	46	77	16	—	7	20
TC-79-02	b	—	2.1621	2.7696	3.2071	2.9855	3.0710	3.0748
	n	—	4	21	9	8	41	24
TC-80-02	b	3.2340	2.7391	2.8600	2.8953	2.7987	3.0275	3.0903
	n	9	15	43	15	6	98	75
TC-80-03	b	3.0348	2.6629	2.9790	3.6220	2.7675	3.0245	3.3476
	n	11	28	26	23	5	175	59
TC-80-04	b	2.9700	3.0016	2.7965	2.8786	3.5380	3.1853	2.9405
	n	12	22	71	11	7	22	45
TC-80-05	b	2.7615	2.8003	2.9636	3.3239	2.9335	3.0145	3.1002
	n	33	39	40	8	11	103	57
TC-81-01	b	3.1423	2.8631	2.8294	3.2541	—	3.0380	2.8785
	n	11	6	35	9	—	16	15
TC-81-02	b	2.8147	2.8850	2.8570	2.9673	2.1396	2.8549	3.0123
	n	11	9	5	3	3	57	38
TC-81-03	b	3.2171	2.8495	2.9983	4.7342	2.8351	3.4360	3.0373
	n	6	11	45	3	3	9	32
TC-81-04	b	2.8019	2.9873	2.7917	3.3846	3.0530	3.0465	2.9848
	n	35	57	75	23	19	112	79
All pooled	b	2.8626	2.9519	2.8281	3.1344	3.0000	3.0215	3.0662
	N	181	267	471	128	84	754	547
	F value	1.3214	1.2750	3.0654*	1.0638	0.4988	1.6198	3.3421*
	d.f.	9, 161	10, 245	10, 449	10, 106	8, 66	10, 732	10, 525

*P ≤ 0.001

TABLE 3. ANCOVA COMPARING THE SLOPES OF LENGTH-WEIGHT RELATIONSHIPS OF DEEPSEA FISHES GROUPED BY AREA OF CAPTURE

Location		*Seriola dumerili*	*Pseudocaranx dentex*	*Pristipomoides filamentosus*	*Pristipomoides sieboldii*	*Pristipomoides zonatus*	*Etelis carbunculus*	*Epinephelus quernus*
Nihoa	Slope (b)	2.0632	2.9491	2.7190	3.3226	2.8226	2.7018	3.1117
	Number (n)	6	17	6	11	4	9	11
Twin Banks	b	3.5030			—		—	2.4642
	n	4			2		2	3
Necker Island	b	3.1249	2.8444	2.8820	3.1665	3.3738	3.0851	2.9346
	n	27	23	138	23	8	62	25
French Frigate Shoals	b	3.0290	2.8800	2.8474	2.5694	2.9584	3.1620	3.0196
	n	10	29	189	25	11	27	70
Brooks Banks	b	—		2.5652				—
	n	1		7				1
St. Rogatien Bank	b	2.6158	2.9327	2.8740	4.2627	—	3.0025	2.7741
	n	4	12	16	3	2	17	21
Gardner Pinnacles	b	2.8590	3.0331	2.9417	3.0694	2.9069	3.0645	3.2203
	n	30	47	24	4	5	19	19
Raita Bank	b	3.0471	3.2211	2.7278	3.7351	3.1793	3.1094	3.0638
	n	15	23	17	16	8	24	47
Maro Reef	b	2.7612	2.9672	2.5130	—	2.6892	2.8013	3.0421
	n	19	29	35	2	9	24	53
Laysan Island	b	3.0085	3.1059	2.5450	3.5621	3.1261	3.0501	3.2619
	n	20	31	25	6	8	50	54
Northampton Seamounts	b		—	—	—	1.0547	2.4400	—
	n		1	1	2	6	6	2
Pioneer Bank	b							4.4152
	n							5

TABLE 3. ANCOVA COMPARING THE SLOPES OF LENGTH-WEIGHT RELATIONSHIPS OF DEEPSEA FISHES GROUPED BY AREA OF CAPTURE (continued)

Location		Seriola dumerili	Pseudocaranx dentex	Pristipomoides filamentosus	Pristipomoides sieboldii	Pristipomoides zonatus	Etelis carbunculus	Epinephelus quernus
Lisianski Island	b	3.0457	—	2.7858	—	—	2.9101	2.8368
	n	4	1	3	1	2	19	16
Bank No. 8	b	2.8226				2.5721	2.9802	3.3047
	n	6				12	46	15
Bank No. 9	b	2.6286	1.4618	—	3.2199	1.5433	2.9547	2.9476
	n	10	3	1	6	3	41	25
Pearl and Hermes Atoll	b	2.8353	2.9894	—	3.0234	2.4107	2.9689	3.0459
	n	19	46	2	12	7	212	111
Salmon Bank	b				2.7487	—	3.0449	—
	n				7	1	38	2
Ladd Seamount	b		-6.3426		0.5139		3.0938	3.5369
	n		3		6		55	18
Midway Islands	b	—	—				2.8397	2.9011
	n	2	1				17	8
Nero Seamount	b	1.0460	—	—	—		2.9148	2.8623
	n	3	1	2	1		77	10
Kure Atoll	b				—		3.3064	3.1142
	n				1		9	20
Bank No. 11	b							3.0171
	n							9
Group	b	2.9109	2.9868	2.8479	3.0656	2.9777	3.0135	3.0624
	n	177	263	460	119	81	752	540
	F value	1.5026	1.8598	1.8689	1.7048	0.9770	1.2153	3.4280*
	d.f.	13, 149	10, 241	9, 440	10, 97	10, 59	17, 716	18, 502

*P ≤ 0.001

TABLE 4. LENGTH-WEIGHT RELATIONSHIPS OF FISHES COMMONLY CAUGHT IN THE DEEPSEA HANDLINE FISHERY IN THE NORTHWESTERN HAWAIIAN ISLANDS

Species	Equation*	Y-axis Intercept	Regression Coefficient	N	Correlation Coefficient	Fork Length	
						Max. (mm)	Min. (mm)
Seriola dumerili	1	2.6069	0.3349	181	0.985	1,138	499
	2	-7.5280	2.8971				
	3	2.6026	0.3400				
	4	-7.6551	2.9412				
Pseudocaranx dentex	1	2.5860	0.3283	267	0.987	890	333
	2	-7.6624	2.9694				
	3	2.5832	0.3325				
	4	-7.7686	3.0074				
Pristipomoides filamentosus	1	2.5852	0.3455	471	0.995	779	234
	2	-7.4085	2.8670				
	3	2.5846	0.3471				
	4	-7.4453	2.8806				
Pristipomoides sieboldii	1	2.5741	0.2758	128	0.929	435	245
	2	-8.0845	3.1327				
	3	2.5772	0.2967				
	4	-8.6857	3.3702				
Pristipomoides zonatus	1	2.5580	0.3026	86	0.965	489	263
	2	-7.8524	3.0751				
	3	2.5559	0.3137				
	4	-8.1477	3.1878				
Etelis carbunculus	1	2.5864	0.3192	754	0.981	635	260
	2	-7.7930	3.0163				
	3	2.5850	0.3253				
	4	-7.9464	3.0740				
Etelis coruscans	1	2.5993	0.3376	44	0.979	880	480
	2	-7.3542	2.8399				
	3	2.5945	0.3448				
	4	-7.5248	2.9003				
Epinephelus quernus	1	2.5912	0.3187	547	0.989	1,106[†]	238
	2	-7.9342	3.0683				
	3	2.5886	0.3223				
	4	-8.0318	3.1028				

*Predictive equation 1: $\log X = \log a + b \log Y$
Predictive equation 2: $\log Y = \log c + d \log X$
Functional equation 3: $\log X = \log u + v \log Y$
Functional equation 4: $\log Y = \log w + x \log X$

where X = fork length (mm)
Y = weight (kg)
Y-intercept: a, c, u, w
regression coefficient: b, d, v, x

[†] Total length

TABLE 5. STANDARD LENGTH-FORK LENGTH RELATIONSHIPS OF FISHES COMMONLY CAUGHT IN THE DEEP-SEA HANDLINE FISHERY IN THE NORTHWESTERN HAWAIIAN ISLANDS

Species	Equation*	Y-axis Intercept	Regression Coefficient	N	Correlation	Range of Fork Length		Range of Standard Length	
						Max. (mm)	Min. (mm)	Max. (mm)	Min. (mm)
Seriola dumerili	1	3.5344	0.9391	74	0.996	1,494	524	1,367	504
	2	2.1377	1.0572						
	3	0.7493	0.9425						
	4	-0.7889	1.0610						
Pseudocaranx dentex	1	-0.1104	0.9448	129	0.997	830	464	772	431
	2	4.6975	1.0510						
	3	-2.2639	0.9481						
	4	2.4134	1.0547						
Pristipomoides filamentosus	1	2.5515	0.9012	200	0.997	779	268	723	242
	2	0.5081	1.1034						
	3	1.0884	0.9037						
	4	-1.1713	1.1065						
Pristipomoides sieboldii	1	4.2166	0.8983	70	0.987	435	245	403	225
	2	4.0474	1.0853						
	3	0.0356	0.9098						
	4	-0.0218	1.0992						

*Prediction equation 1: $X = a + b Y$
Prediction equation 2: $Y = c + d X$
Functional equation 3: $X = u + v Y$
Functional equation 4: $Y = w + y X$

where X = standard length
Y = fork length
Y-intercept: a, c, u, w
regression coefficient: b, d, v, y

TABLE 5. STANDARD LENGTH-FORK LENGTH RELATIONSHIPS OF FISHES COMMONLY CAUGHT IN THE DEEP-SEA HANDLINE FISHERY IN THE NORTHWESTERN HAWAIIAN ISLANDS (continued)

Species	Equation	Y-axis Intercept	Regression Coefficient	N	Correlation	Range of Fork Length		Range of Standard Length	
						Max. (mm)	Min. (mm)	Max. (mm)	Min. (mm)
Pristipomoides zonatus	1	-13.888	0.9506	42	0.985	489	282	452	256
	2	26.825	1.0207						
	3	-20.0176	0.9650						
	4	20.7707	1.0362						
Etelis carbunculus	1	-2.8201	0.9185	434	0.993	629	269	581	241
	2	9.8694	1.0728						
	3	-6.0045	0.9253						
	4	6.5023	1.0807						
Etelis coruscans	1	-0.5400	0.9169	40	0.998	480	876	440	810
	2	3.4976	1.0859						
	3	-1.8766	0.9189						
	4	2.0160	1.0883						
Epinephelus quernus	1	-13.152	0.8630	289	0.997	21,100	235	956	181
	2	18.896	1.1525						
	3	-14.758	0.8653						
	4	17.096	1.1556						

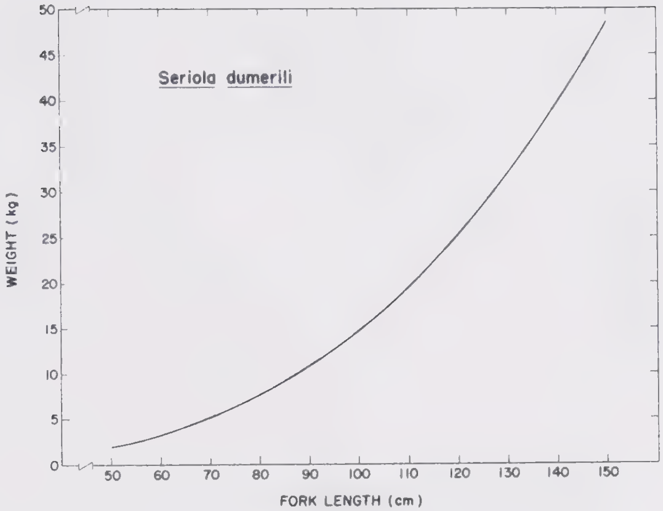

Figure 1. Functional length-weight relationship of the greater amberjack from the Northwestern Hawaiian Islands

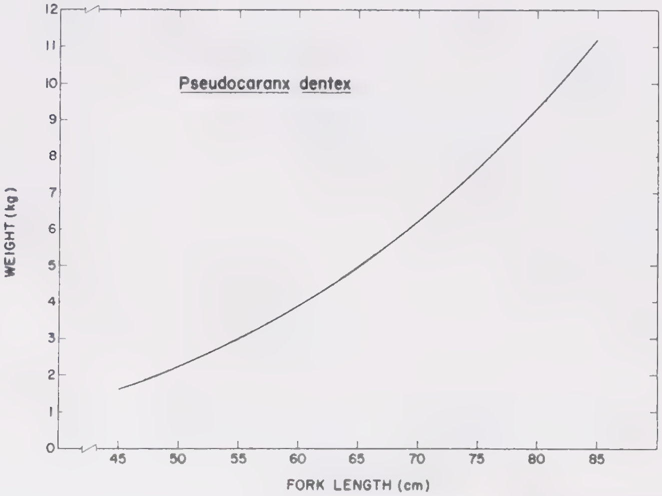

Figure 2. Functional length-weight relationship of pig ulua from the Northwestern Hawaiian Islands

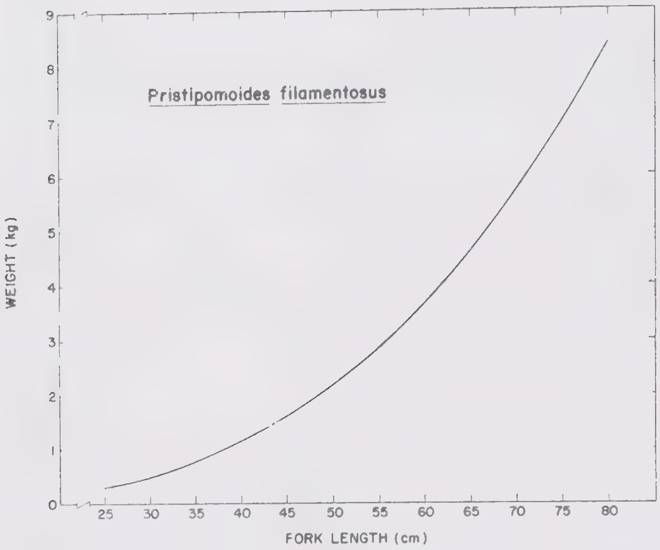

Figure 3. Functional length-weight relationship of opakapaka from the Northwestern Hawaiian Islands

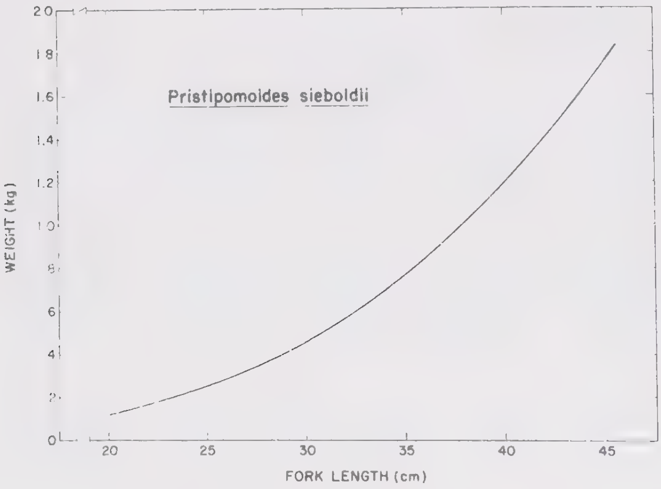

Figure 4. Functional length-weight relationship of kalekale from the Northwestern Hawaiian Islands

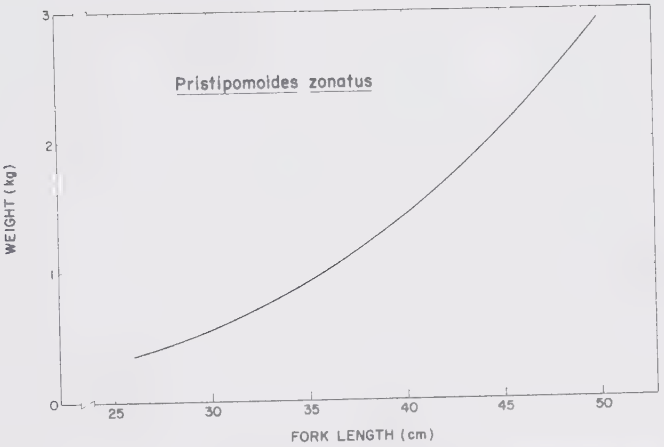

Figure 5. Functional length-weight relationship of gindai from the Northwestern Hawaiian Islands

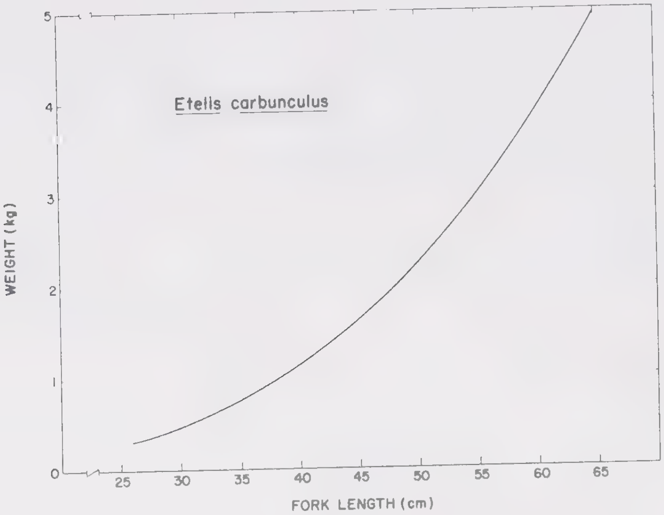

Figure 6. Functional length-weight relationship of ehu from the Northwestern Hawaiian Islands

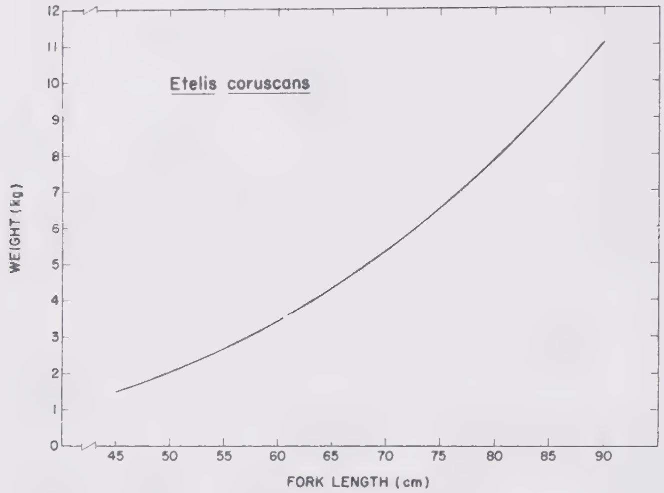

Figure 7. Functional length-weight relationship of onaga from the Northwestern Hawaiian Islands

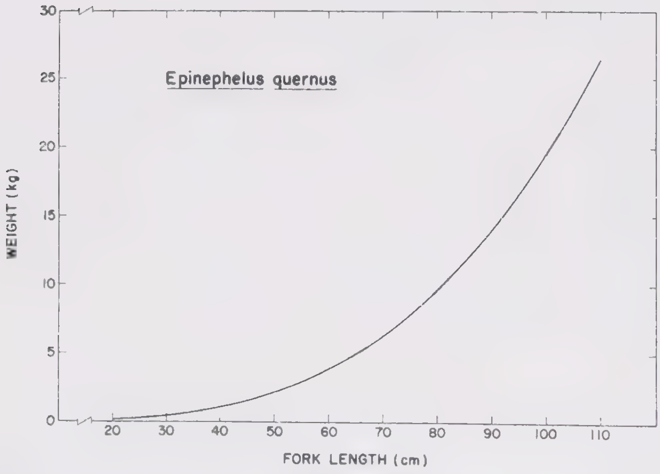

Figure 8. Functional length-weight relationship of hapuupuu from the Northwestern Hawaiian Islands

DISCUSSION

The slopes of length-weight regressions were compared among groups by ANCOVA to test for equality of slopes in the data. There were no significant differences between the slopes of male and female groups for any species (Table 1). Sex comparison for hapuupuu was not conducted due to the small sample size for males. No significant differences occurred in the comparison of slopes among cruises except for opakapaka and hapuupuu (Table 2). Large opakapaka caught on cruises 78-03 and 80-03 and small opakapaka caught on cruise 81-03 appeared to have been responsible for the significant difference. The slope of the length-weight regression of opakapaka of cruise 78-03 was lower than the rest of the cruises and the slopes for cruises 80-03 and 81-03 were higher than the other cruises. Likewise, large hapuupuu caught on cruise 80-03 appeared to be responsible for the significant difference among cruises. These cruises occurred during different months of the year, so the nonsignificance may also have implied that there were no significant seasonal differences in their length-weight relations. No significant differences were found in the comparison of slopes among banks for all species except hapuupuu (Table 3). Hapuupuu has a stout body compared with the more elongated body type of the snappers and greater amberjack or the laterally compressed body of pig ulua, and its length-weight relations may reflect changes in size structure in its population more than the other bottomfishes.

Forster et al. (1970) estimated the length-weight relationship of ehu from the western Indian Ocean. They found that females grew larger than males, calculated the length-weight relationship separately for males and females, and provided 95 percent confidence limits of the exponent of L (length). Although most of the Indian Ocean specimens were larger than Hawaiian forms (largest: 111 cm in the Indian Ocean, 63 cm in the NWHI), the estimates of the exponent of L for the two areas agreed well for males (3.07) and were well within the confidence limits ($P = 0.05$) of the exponent of L for females. Female fish in Hawaii also grew slightly larger, but the difference was not statistically significant.

Ralston (1981) calculated the length-weight relationship of opakapaka from the NWHI, from data collected on a commercial fishing vessel using a spring scale to weigh the fish. The parameters could not be directly compared, so curves derived from the parameters were compared and found to be only slightly different. Weights estimated for lengths <70 cm FL were slightly larger by Ralston's parameters.

Burch (1979) calculated the length-weight relationship of the greatest amberjack caught by sport fishing boats at Miami, Florida. Hawaii data could not be compared directly because different units of measurements were used, so curves derived from the parameters were compared and found to be slightly different. Weights estimated by Burch's formula tended to be lower than Hawaiian estimates, with the difference increasing as length increased. The weight difference estimated for a 130-cm FL fish by the two formulae was about 2.5 kg. The difference in length-weight relationships may have been due to unequal fish sizes in the two studies. The catch in the NWHI consisted mostly of fish under 100-cm FL, whereas the catch in Florida consisted primarily of fish greater than 100-cm FL. Other possible reasons for the difference in length-weight relationships may have been real morphometric differences between populations in different geographical areas or unequal dehydration due to sampling methods. Burch weighed his samples at the dock after a day's fishing trip, whereas Hawaiian samples were weighed within 2 hours after being caught.

SUMMARY

Length-weight data for each species except onaga were separated into groups by sex, cruise, and area of capture. The slope of length-weight relationship of a group was compared with others within their grouping by ANCOVA to test for heterogeneity in the data. Results of the tests appeared to justify the pooling of all data for each species.

Parameters of both the functional and predictive equations of length-weight relationship and standard length-fork length relationship were calculated for greater amberjack, pig ulua, opakapaka, kalekale, gindai, ehu, and onaga. For hapuupuu, the parameters for standard length-total length and length-weight relationships were calculated. In this paper, length-weight relationships are given for eight major deepsea species caught by handline in the NWHI. These data represent conversion factors that should prove to be useful in the development of fishery management plans for the Hawaiian handline fishery.

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LIFE HISTORY, DISTRIBUTION, AND ABUNDANCE OF BOTTOMFISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

Relative apparent abundance of the eight most important bottomfish species was examined for the major banks of the Northwestern Hawaiian Islands. Most noteworthy was the dominance of *Pristipomoides filamentosus* at Necker bank, French Frigate Shoals, and Brooks Banks and of *Etelis carbunculus* northwest of Lisianski bank. In general, catch rates and mean sizes increased at the northwestern end of the archipelago. Research on age and growth, length-weight relationships, reproductive biology, feeding habits, and the occurrence of ciguatoxin in bottomfishes was also reviewed.

age and growth
relative apparent abundance
bottomfishes
species composition

INTRODUCTION

The history of the fishery for snappers, grouper, and jacks, commonly referred to as bottomfishes, in the Northwestern Hawaiian Islands (NWHI) is not well documented. This fishery has been in existence in the NWHI at least since the mid-1940s (A.B. Amerson, 1971) and perhaps as early as the 1930s (see paper in this proceedings by Hau). From records maintained by the Division of Aquatic Resources (DAR), Hawaii Department of Land and Natural Resources, summaries of total annual catch, fishing effort (boat trip), and ex-vessel value per year were prepared for the period 1959 through 1977 by Polovina and Moffitt (1980) (Table 1). Annual catch statistics by species were also tabulated. During this period one vessel accounted for 95.5 percent of the catch. Starting in November 1976, a spiny lobster fishery developed in the NWHI; in addition to lobsters, vessels in this fishery landed bottomfishes. When the jig boat albacore fishery expanded to the central North Pacific in 1979, some trolling vessels remained in Hawaii beyond the season for albacore and converted to bottomfishing in the NWHI.

TABLE 1. TOTAL VALUE, WEIGHT OF CATCH, AND NUMBER OF TRIPS IN THE BOTTOM HANDLINE FISHERY IN THE NORTHWESTERN HAWAIIAN ISLANDS

Year	Dollar Value	Kilograms Caught	Number of Trips
1959	26,896	32,164	10
1960	45,779	49,515	16
1961	30,115	34,476	11
1962	25,363	29,244	13
1963	32,653	40,730	18
1964	39,277	47,260	19
1965	20,118	25,154	9
1966	18,213	21,935	9
1967	13,775	14,822	6
1968	14,320	15,172	6
1969	14,812	18,113	4
1970	39,147	33,683	11
1971	50,206	34,180	17
1972	41,992	19,356	17
1973	62,759	28,050	20
1974	48,899	22,313	15
1975	63,873	27,012	14
1976	78,476	26,730	14
1977	95,659	35,576	20

Source: Polovina and Moffitt, 1980

In March 1977 the Magnuson Fishery Conservation and Management Act (FCMA) of 1976 extended federal jurisdiction over fishery resources from 3 to 200 nautical miles (nmi) around the islands in the Hawaiian Archipelago (Figure 1). The FCMA also established eight regional fishery management councils nationally to manage the resources in the fishery conservation zone (FCZ). The Western Pacific Regional Fishery Management Council was established with jurisdiction in the FCZs around Hawaii, Guam, Northern Marianas, and American Samoa and is currently examining the fishery for bottomfishes to determine whether a fishery management plan (FMP) is warranted.

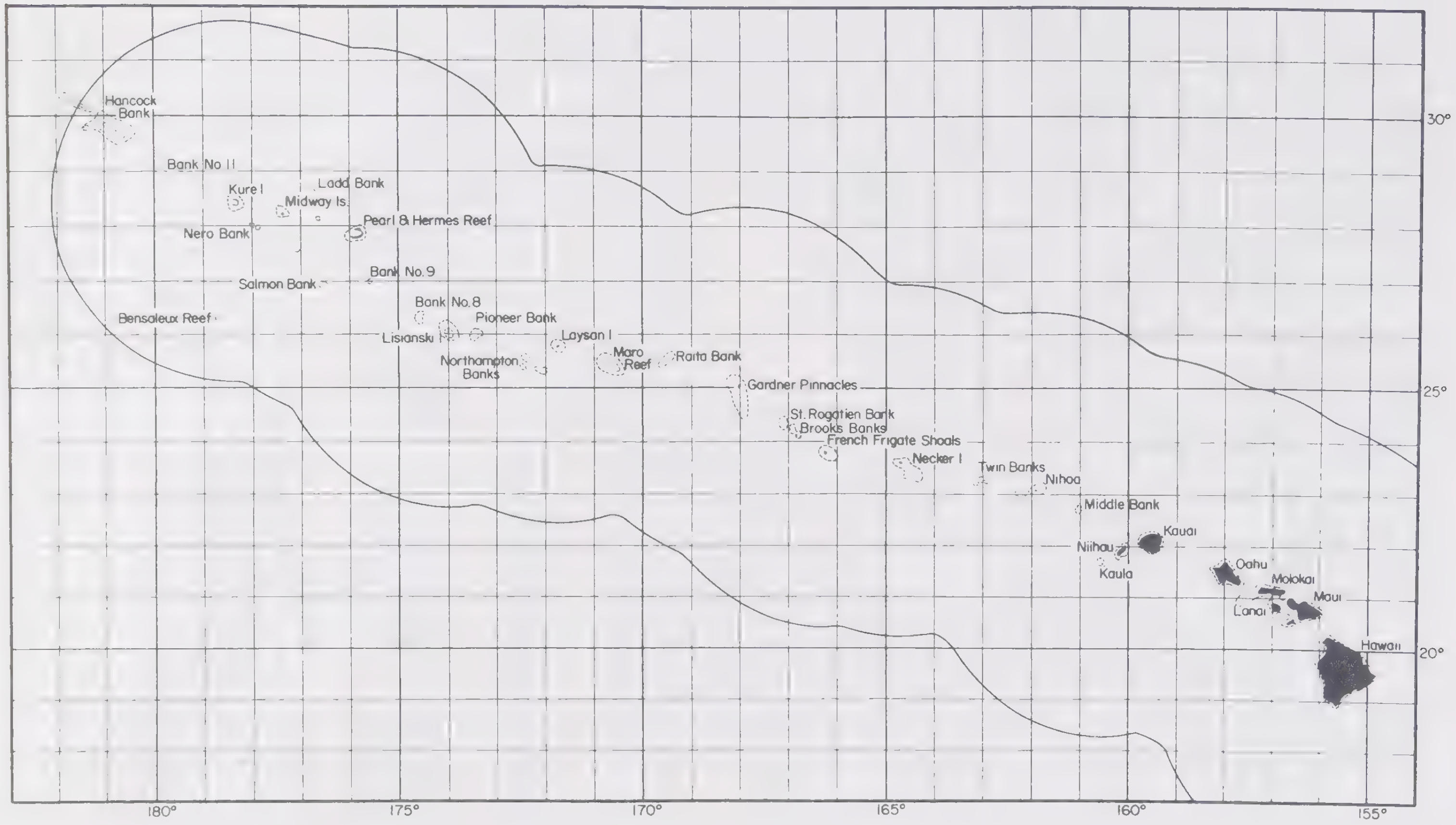
Hancock Bank
Bank No 11
Kure I
Ladd Bank
Midway Is.
Pearl & Hermes Reef
Nero Bank
Bank No. 9
Salmon Bank
Bank No. 8
Pioneer Bank
Bensaleux Reef
Lisianski I
Laysan I
Northampton Banks
Maro Reef
Raita Bank
Gardner Pinnacles
St. Rogatien Bank
Brooks Banks
French Frigate Shoals
Necker I
Twin Banks
Nihoa
Middle Bank
Kauai
Niihau
Kaula
Oahu
Molokai
Maui
Lanai
Hawaii
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1. The U.S. Fishery Conservation Zone around the Hawaiian Archipelago

Because very little was known about the biotic resources in the NWHI, a cooperative research agreement was signed by the Division of Aquatic Resources; the Fish and Wildlife Service (FWS), U.S. Department of Interior; and the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service (NMFS) in 1977 to survey the resources. A year after the formation of the cooperative tripartite agreement, a fourth agency, the University of Hawaii Sea Grant College Program, became an active participant in the resource investigations. In the agreement, FWS was given the responsibility to survey and assess the terrestrial resources such as sea and land birds, DAR was assigned the assessment of inshore fishery resources, and NMFS was assigned the assessment of offshore fishery resources. Later, NMFS also assumed the responsibility for research on the Hawaiian monk seal, *Monachus schauinslandi*, and the Hawaiian green turtle, *Chelonia mydas*.

Among the offshore fishery resources are the bottomfishes. Various studies were conducted by NMFS to determine their distribution and relative abundance in the NWHI. Studies on age and growth, reproduction, feeding habits, and the occurrence of ciguatoxin in bottomfishes were also conducted. This paper is a review of the results of these studies conducted by the Honolulu Labortory since 1976.

SPECIES OF THE SNAPPER-GROUPER-JACK COMPLEX

The scientific names of bottomfish species commonly caught in the NWHI are listed in Table 2 along with synonyms and Hawaiian or local names which have remained in use for many decades. The fishes in the snapper-grouper-jack complex are also called deepsea handline fishes, but are referred to as bottomfish in this paper.

DISTRIBUTION AND APPARENT ABUNDANCE

A primary objective of the NMFS NWHI study was to conduct assessments of the resources in the area. Catch data at 283 handline stations were collected from the R/V *Townsend Cromwell* from October 1976 to September 1982. Effort was recorded as line-hour and catch as either the number or weight of fish.

Bottomfishes were widely distributed throughout the NWHI (Table 3). To determine their vertical distribution, traps, trawls, and handlines were used to sample various depths. The depth range of the various species was tabulated for each bank (Table 3) by Uchida and Uchiyama (in preparation). The true depth range for these species is probably wider than that estimated by the catch data.

TABLE 2. SCIENTIFIC NAME, SYNONYM, AND LOCAL NAME OF NORTHWESTERN HAWAIIAN ISLANDS BOTTOMFISHES

Scientific Name	Synonym	Local Name
Serranidae		
Epinephelus quernus		Hapuupuu
Carangidae		
Carangoides orthogramus[1]	*C. ferdau*	Ulua
Caranx ignoblis		Ulua
C. lugubris		Ulua
C. melampygus		Omilu
Pseudocaranx dentex[2]	*C. cheilio*	Pig ulua
Seriola dumerili		Kahala
S. lalandii		Kahala opio
Lutjanidae		
Aprion virescens		Uku
Etelis carbunculus[3]	*E. marshi*	Ehu
E. coruscans[3]	*E. carbunculus*	Onaga
Pristipomodies filamentosus[4]	*P. microlepis*	Opakapaka
P. sieboldii		Kalekale
P. zonatus[5]	*Rooseveltia brighami*	Gindai
Scorpaenidae		
Pontinus macrocephalus[6]	*Merinthe macrocephala*	Nohu

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[1] Misidentification corrected by F.W. Smith-Vaniz (Randall, 1980)

[2] Revised by F.W. Smith-Vaniz, The Academy of Natural Sciences, Philadelphia, PA 19103, personal communication, 1981

[3] Revised by Anderson (1981)

[4] Revised by Kami (1973)

[5] Change proposed by W.D. Anderson, College of Charleston, Charleston, SC 29412, personal communication, 1981

[6] Revised by Eschmeyer and Randall (1975)

TABLE 3. DEPTH DISTRIBUTION (IN METERS) BY BANK OF BOTTOM FISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS DURING RESOURCE SURVEYS FROM OCTOBER 1976 TO AUGUST 1981

Bank	*Epinephelus quernus*		*Pseudocaranx dentex*		*Seriola dumerili*		*Etelis carbunculus*		*E. coruscans*		*Pristipomoides filamentosus*		*P. sieboldii*		*P. zonatus*	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Middle Bank	146	146	—	—	44	146	—	—	—	—	36	73	—	—	—	—
Nihoa	44	183	*	*	51	73	128	201	—	—	*	*	137	137	—	—
Twin Banks	183	183	27	46	29	91	183	183	256	256	—	—	91	91	—	—
Necker Island	27	229	66	174	2	229	139	229	*	*	31	328	110	120	183	183
French Frigate Shoals	58	194	110	165	26	186	113	152	—	—	46	186	113	201	128	128
Brooks Banks	183	183	—	—	51	201	—	—	—	—	36	161	—	—	201	201
St. Rogatien Bank	—	—	*	*	*	*	*	*	*	*	*	*	—	—	—	—
Gardner Pinnacles	110	347	16	183	16	128	128	183	*	*	27	183	128	128	—	—
Raita Bank	31	172	183	183	146	146	—	—	—	—	40	40	172	183	—	—
Maro Reef	38	201	102	201	2	201	102	201	—	—	31	183	102	102	102	201
Laysan Island	90	183	146	174	2	183	174	201	256	256	64	174	*	*	201	201
Northampton Seamounts	164	219	201	201	—	—	110	219	—	—	110	201	146	201	164	201
Lisianski Island and Pioneer	110	238	27	194	110	247	179	238	194	194	91	179	194	194	183	238
Bank No. 8	146	183	—	—	146	165	219	238	—	—	71	71	—	—	183	183
Pearl and Hermes Atoll	33	238	48	238	35	238	121	271	183	229	57	164	164	198	146	183
Salmon Bank	119	119	—	—	—	—	119	219	—	—	—	—	219	219	—	—
Ladd Island	66	216	*	*	—	—	146	216	—	—	—	—	146	216	—	—
Midway Islands	26	219	0	183	2	128	192	219	—	—	—	—	—	—	—	—
Nero and Pogy	146	146	183	183	111	111	183	183	—	—	108	108	—	—	—	—
Kure Atoll	18	218	2	183	9	9	219	219	183	183	—	—	*	*	—	—

Note: Information abstracted from Table 2 of Uchida and Uchiyama (in preparation)
* Depth uncertain

The catch rates varied among banks (Table 4). The catch rate of hapuupuu generally increased with distance away from the high islands. For pig ulua, the catch rate was high around Raita Bank, Maro bank, and Laysan bank, whereas for kahala, it was high from Gardner Pinnacles to Pearl and Hermes Atoll. West of Lisianski bank, the relative abundance of ehu increased greatly. Opakapaka were abundant at Necker bank and French Frigate Shoals but were not caught west of Nero Seamount. Although this species was not recorded at Midway bank, it is known to occur there (S. Ralston, 1983: personal communication). Furthermore, opakapaka were caught in lobster pots at bank no. 8, although none were caught on handlines. The relative abundance figures for onaga, kalekale, and gindai were too low to analyze by locality.

Species composition at each bank is presented in Table 5. Miscellaneous species listed previously by Moffitt (1980) were not included. A noticeable feature of species composition in the NWHI was the dominance of ehu west of Lisianski bank and opakapaka at Necker bank, French Frigate Shoals, and Brooks Banks. Catches west of Lisianski bank were composed of 45.6 to 86.5 percent ehu, excluding data from Midway Islands and Kure Atoll. Opakapaka represented 44.4 percent of the catch at Necker bank, 52.5 percent at French Frigate Shoals, and 40.0 percent at Brooks Banks. No gindai were caught west of Ladd Seamount. This pattern of species composition by banks was similar to that reported by Moffitt (1980).

For each species the fork or total lengths from all banks were pooled and compared by one-way analysis of variance. Mean sizes for seven species at the various banks varied significantly (Table 6). In general, significant differences in fish size existed between banks that were heavily fished and those that were pristine (NMFS, unpublished data). Because the fishes were larger on the northwestern end of the archipelago (except for pig ulua), it was not surprising that catch rates (kilograms per line-hour) also increased at that end of the NWHI (Table 7).

Catch and effort data to estimate sustainable yield from production analysis were unavailable for the NWHI. Annual maximum sustainable yields (MSY) of 111,300 kg for Oahu and 288,320 kg for Maui, Molokai, and Lanai have been estimated (Ralston, 1980; Ralston and Polovina, 1982; Polovina and Moffitt, 1980). These original estimates have since been revised. Assuming that abundance and population dynamics of these species are similar in the NWHI and the main Hawaiian islands, the MSY was estimated for these species in the NWHI (see paper in this proceedings by Ralston).

LIFE HISTORY STUDIES

Otoliths were collected for age and growth studies, gonads for reproductive studies, stomach contents and spew samples for feeding habit studies, and various tissue samples for ciguatoxin studies.

TABLE 4. SUMMARY OF CATCH RATES (NUMBER PER LINE-HOUR) FOR BOTTOMFISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Bank	Total Effort (Line-Hours)	*Epinephelus quernus*	*Pseudocaranx dentex*	*Seriola dumerili*	*Etelis carbunculus*	*E. coruscans*	*Pristipomoides filamentosus*	*P. sieboldii*	*P. zonatus*
Middle Bank	9.73	0.21	—	0.10	—	—	—	—	—
Nihoa	168.75	0.12	0.10	0.04	0.50	0.01	0.06	0.19	0.02
Twin Banks	29.47	0.10	—	0.14	0.07	0.03	0.07	0.07	—
Necker Island	363.85	0.14	0.08	0.11	0.33	0.00	0.63	0.08	0.04
French Frigate Shoals	297.17	0.33	0.18	0.12	0.11	0.00	1.05	0.10	0.10
Brooks Banks	61.27	0.05	—	0.03	—	—	0.07	—	0.02
St. Rogatien Bank	49.07	0.43	0.29	0.08	0.35	0.20	0.37	0.06	0.04
Gardner Pinnacles	117.62	0.16	0.15	0.16	0.16	0.03	0.14	0.03	0.04
Raita Bank	94.35	0.49	0.24	0.17	0.25	0.17	0.18	0.17	0.08
Maro Reef	101.47	0.55	0.40	0.22	0.24	—	0.45	0.02	0.10
Laysan Island	175.40	0.42	0.31	0.18	0.36	0.02	0.19	0.05	0.08
Northampton Seamounts	16.60	0.12	0.06	—	0.42	—	0.12	0.18	0.54
Lisianski Island and Pioneer	93.57	0.50	0.07	0.14	0.27	0.06	0.10	—	0.04
Bank No. 8	39.27	0.38	—	0.15	1.17	—	—	—	0.33
Pearl and Hermes Atoll	229.93	0.74	0.22	0.16	1.72	0.12	0.03	0.10	0.03
Salmon Bank	41.60	0.05	—	—	0.75	—	—	0.17	0.02
Ladd Island	52.80	0.15	—	—	1.04	0.04	—	0.09	—
Midway Islands	26.83	0.82	0.45	0.04	0.75	—	—	—	—
Nero and Pogy	18.80	0.53	0.05	—	4.10	—	—	0.05	—
Kure Atoll	75.33	0.42	0.20	0.01	0.20	0.03	—	0.01	—

TABLE 5. SPECIES COMPOSITION (PERCENTAGE) OF BOTTOMFISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Bank	*Epinephelus quernus*	*Pseudocaranx dentex*	*Seriola dumerili*	*Etelis carbunculus*	*E. coruscans*	*Pristipomodies filamentosus*	*P. sieboldii*	*P. zonatus*
Middle Bank	66.7	—	33.3	—	—	—	—	—
Nihoa	11.5	9.8	3.4	48.3	0.6	5.7	18.3	2.2
Twin Banks	21.4	—	28.6	14.3	7.2	14.3	14.3	—
Necker Island	10.2	5.7	7.7	23.5	0.2	44.4	5.5	2.8
French Frigate Shoals	16.5	8.9	5.9	5.7	0.2	52.5	5.2	5.0
Brooks Banks	30.0	—	20.0	—	—	40.0	—	10.0
St. Rogatien Bank	23.6	15.7	4.5	19.1	11.2	20.2	3.4	2.2
Gardner Pinnacles	18.1	17.1	18.1	18.1	3.8	16.2	3.8	4.8
Raita Bank	27.7	13.8	9.6	14.4	9.6	10.2	9.6	4.8
Maro Reef	27.9	20.4	10.9	11.9	—	22.9	1.0	5.0
Laysan Island	26.1	19.4	11.0	22.6	1.4	11.7	2.8	4.9
Northampton Seamounts	8.3	4.2	—	29.2	—	8.3	12.5	37.5
Lisianski Island and Pioneer	35.3	5.3	9.8	18.8	4.5	6.8	0.8	3.0
Bank No. 8	18.8	—	7.5	57.5	—	—	—	16.2
Bank No. 9	27.8	3.3	11.1	45.6	1.1	1.1	6.6	3.3
Pearl and Hermes Atoll	23.6	6.9	5.0	54.5	3.8	1.0	3.3	1.0
Salmon Bank	4.9	—	—	75.6	—	—	17.0	2.4
Ladd Island	11.4	—	—	78.6	2.8	—	7.1	—
Midway Islands	31.4	17.1	1.4	28.6	—	—	—	—
Nero and Pogy	11.2	1.1	—	86.5	—	—	1.1	—
Kure Atoll	48.5	22.7	1.5	22.7	3.0	—	1.5	—

TABLE 6. ONE-WAY ANALYSIS OF VARIANCE COMPARING MEAN LENGTHS OF SEVEN SPECIES OF BOTTOMFISHES

Species	Degrees of Freedom	F Value	Probability
Epinephelus quernus	18, 521	6.3347	0.0186
Pseudocaranx dentex	10, 252	6.8400	0.0
Seriola dumerili	13, 163	3.4110	0.0001
Etelis carbunculus	17, 734	6.6013	0.0
Pristipomoides filamentosus	9, 450	26.6070	0.0
P. sieboldii	10, 108	2.2649	0.0191
P. zonatus	10, 70	2.3507	0.0186

TABLE 7. SUMMARY OF CATCH RATES (KILOGRAMS PER LINE-HOUR) FOR BOTTOMFISHES IN THE NORTHWESTERN HAWAIIAN ISLANDS

Bank	*Epinephelus quernus*	*Pseudocaranx dentex*	*Seriola dumerili*	*Etelis carbunculus*	*E. coruscans*	*Pristipomoides filamentosus*	*P. sieboldii*	*P. zonatus*	Total
Middle Bank	0.92	—	0.42	—	—	—	—	—	1.34
Nihoa	0.52	0.52	0.26	0.77	0.04	0.25	0.13	0.03	2.52
Twin Banks	1.20	—	1.79	0.15	0.21	—	0.08	—	3.43
Necker Island	0.72	0.38	0.59	0.43	0.01	1.69	0.06	0.05	3.93
French Frigate Shoals	2.02	1.11	0.64	0.17	0.01	2.71	0.07	0.15	6.88
Brooks Banks	0.30	—	0.24	—	—	0.18	—	0.02	0.74
St. Rogatien Bank	3.11	1.93	0.79	0.52	0.65	1.37	0.04	0.06	8.47
Gardner Pinnacles	0.87	0.87	1.02	0.29	0.15	0.63	0.02	0.06	3.91
Raita Bank	3.81	1.61	1.33	0.54	0.90	0.80	0.12	0.16	9.27
Maro Reef	3.07	1.74	1.39	0.50	—	1.87	0.06	0.18	8.81
Laysan Island	3.67	2.05	1.40	0.69	0.10	1.10	0.02	0.14	9.17
Northampton Seamounts	1.25	0.54	0.10	0.84	—	0.55	—	1.02	4.30
Lisianski and Pioneer	3.49	0.62	1.31	0.64	0.30	0.45	0.00	0.08	6.89
Bank No. 8	3.95	—	1.41	2.58	—	—	—	0.51	8.45
Bank No. 9	11.85	0.70	4.37	3.29	0.28	0.16	0.17	0.22	21.04
Pearl and Hermes Atoll	4.07	1.20	1.45	2.97	0.65	0.15	0.07	0.07	10.63
Salmon Bank	0.58	—	—	1.63	—	—	0.10	0.03	2.34
Ladd Island	1.75	—	—	2.39	0.32	—	0.10	—	4.56
Midway Islands	3.94	1.79	0.41	1.53	—	—	—	—	7.67
Nero and Pogy	3.91	0.28	—	8.19	—	—	0.04	—	12.42
Kure Atoll	2.90	1.05	0.10	0.51	0.10	—	0.01	—	4.67

Age and Growth

Considerable effort has been expended in estimating age and growth of NWHI bottomfishes (Figure 2). All species were aged by enumerating daily increments on otoliths; two species were aged by counting the annuli. Evidence that increments are deposited daily was obtained only for the pig ulua (Uchiyama et al., in preparation). It is highly improbable that daily increments can be validated for species such as ehu, gindai, kalekale, and onaga that live at great depths. Thus, age and growth estimates are considered tentative for species in which daily increments were not validated.

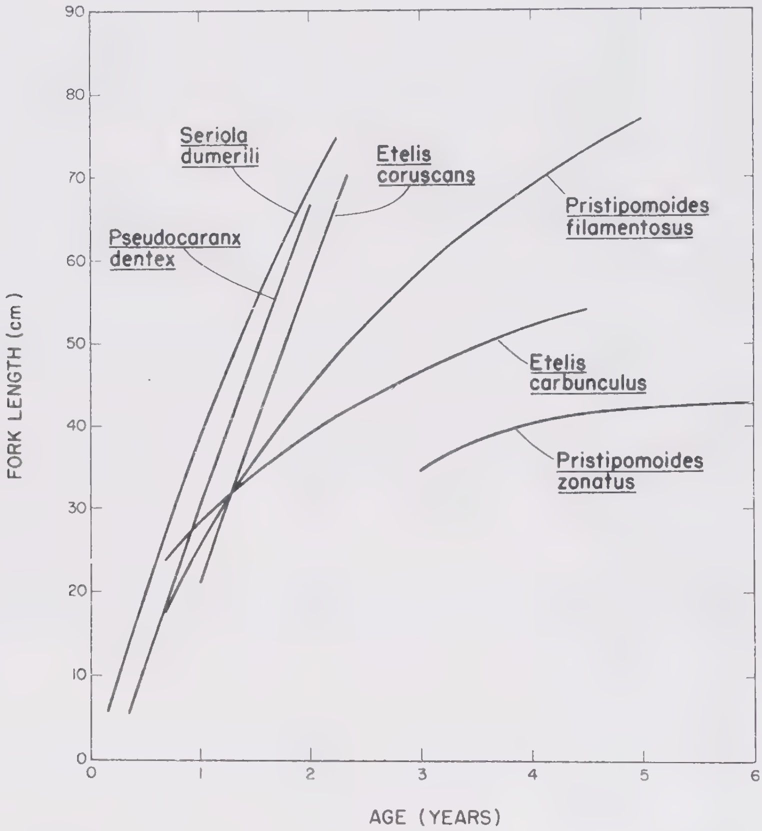

Figure 2. Estimated growth curves of the bottomfishes in the Northwestern Hawaiian Islands

Von Bertalanffy growth parameters (L_∞ = 97.1 cm, k = 0.31, t_0 = 0.02 yr) and a growth curve for opakapaka (Figure 2) were determined from age data (Uchiyama et al., in preparation). Annuli were validated by showing that they were formed at the same time (early summer) each year. The method was validated by comparing back calculated length at age with length at age of the von Bertalanffy growth curve. Annual marks make it possible to age more fish in less time and to age older fish. It was difficult to age opakapaka beyond 3 years with daily increment counts. Age determination by enumeration of daily increments agreed well with the growth curve based on annuli (Uchiyama et al., in preparation).

In need of a faster way to age fish using daily increments, Ralston and Miyamoto (in press) analytically integrated otolith growth rate to estimate age-length relationships. Their estimates of opakapaka age-length relationship suggested growth at 33 to 50 percent of the estimated rate determined by Uchiyama et al. (in preparation). R.L. Radtke (unpublished manuscript) enumerated daily increments on opakapaka otoliths with scanning electron microscopy. His estimates of the age-length relationship were similar to those of Uchiyama et al. (in preparation) for fish of 20 to 56-cm fork length (FL). His age estimates for fish greater than 60-cm FL were higher than those of Uchiyama et al. (in preparation), but lower than those estimated by Ralston and Miyamoto (in press).

Preliminary von Bertalanffy parameters (L_∞ = 43.1 cm, k = 1.09, t_0 = 1.51 yr) and a growth curve (Figure 2) were also estimated for gindai using annual marks (J.H. Uchiyama, unpublished data). However, due to a small sample size the annual marks were not validated. Only three age determinations were made using daily increment counts. These points were within the length ranges of estimated year classes.

All other species were aged by daily increments only. Von Bertalanffy parameters and growth curves were estimated for ehu (L_∞ = 63.9 cm, k = 0.36, t_0 = -0.60 yr) and kahala (L_∞ = 149.4, k = 0.31, t_0 = 0.04 yr) (Uchiyama et al., in preparation) (Figure 2). The estimated L_∞ of ehu (63.9 cm) was very close to the size of the largest ehu (63.5-cm FL) caught during the survey cruises. Ehu in the NWHI appeared not to grow as large as those from New Caledonia [105 cm, 19.0 kg; (R. Grandperrin, 1982: personal communication)] and the Indian Ocean (Forster et al., 1970). The estimated L_∞ of kahala (149.4 cm) was also very close to the size of the largest kahala (149.0-cm FL) caught during the survey cruises. Kahala are known to grow up to 155 cm off Florida (Burch, 1979).

Only linear growth stanzas were calculated for onaga (J.H. Uchiyama, unpublished data) and pig ulua (Uchiyama et al., in preparation) because the largest fish for either species examined had not reached the asymptotic growth phase (Figure 2). Furthermore, no attempt was made to estimate growth of onaga, kahala, and pig ulua beyond the ages indicated in Figure 2 because the otoliths of older fish were not readable. The nucleus of the sagittae of larger fish became very opaque after age 2 and did not allow an accurate enumeration of daily growth increments.

Length-weight Relationships

Predictive and functional length-weight relationships have been calculated from lengths and weights of hapuupuu, ehu, onaga, opakapaka, kalekale, gindai, pig ulua, and kahala caught in the NWHI (see Table 4 of paper in this proceedings by Uchiyama et al.). For all species except onaga, the data were separated into groups by sex, cruise, and location of capture, and the slopes of the regression for each grouping were compared by ANCOVA. No significant differences in slopes between sexes were found for ehu, opakapaka, kalekale, gindai, pig ulua, and kahala. Slopes between sexes were not tested for hapuupuu. Among cruises, significant differences were found for hapuupuu and opakapaka. Since these two species are the most important in the NWHI handline fishery, changes in size composition may have caused the slopes to differ over a period of time. Unusually large or small opakapaka and hapuupuu caught during several cruises could have caused the significantly different slopes among cruises. Among locations, differences in slopes were not significant, except for hapuupuu. The body of hapuupuu is stout, compared with the elongated or laterally compressed body types of the other bottomfish species, which may result in a greater change in weight per unit of length.

Reproduction

Studies on reproduction of bottomfishes have centered on determining spawning seasons, size at sexual maturity, and fecundity. The spawning season was determined by the seasonal distribution of mean gonadal somatic indices. Kahala was found to spawn at a low level throughout the year, with increased activity between February and July and peaking in March and April (see paper in this proceedings by Kikkawa and Everson). Opakapaka spawning peaked in August (ripe ovaries were collected from June through December) (see paper in this proceedings by Kikkawa). Ehu spawned from May through October, peaking from July through September (see paper in this proceedings by Everson). The spawning season for kalekale was from June through September, peaking in August and September; whereas for onaga it was estimated to be in August and September based on ovaries collected primarily in the summer (A.R. Everson, 1983: personal communication). Ripe ovaries of gindai were collected in August, whereas those of pig ulua were collected in January and July and those of hapuupuu in January and February. There appeared to be a serial succession of spawning peaks by species groups: hapuupuu in the winter months, carangids in spring and early summer, and snappers in late summer.

Size at maturity has been determined for three species. Gonads began to develop when the kahala reached a length of 72 cm, and the smallest female with ripe ovaries was 78 cm long (see paper in this proceedings by Kikkawa and Everson). For opakapaka, the ovaries generally began to develop when the females were about 42.5 cm long. The females generally reached spawning condition at a length of about 48.7 cm, although the smallest female with a ripe ovary was only 38.4 cm long (see paper in this proceedings by Kikkawa). The ehu reached sexual maturity at a length of about 29.8 cm and spawned at about 31.8 cm (see paper in this proceedings by Everson). In terms of age, kahala reached sexual maturity at about 2.1 years and began spawning at about 2.4 years. Opakapaka reached sexual maturity at about 1.8 years and generally spawned at about 2.2 years. The ehu was about 1.1 years when it reached sexual maturity and spawned at about 1.2 years.

Fecundity for the same three species was estimated following the method of Van Dalsen (1977). The smallest examined kahala (83.0 cm long) yielded about 1.3 million eggs at one spawning and the largest (118.6 cm long) about 4.0 million eggs (see paper in this proceedings by Kikkawa and Everson). The relationship between the number of eggs spawned and length was linear. The smallest examined opakapaka (48.7 cm long) yielded about 457,090 eggs, at one spawning and the largest (76.3 cm long) about 1,461,875 eggs (see paper in this proceedings by Kikkawa). The relationship between eggs spawned and length for this species was curvilinear. The smallest examined ehu (38.3 cm long) yielded about 349,500 eggs at one spawning and the largest (50.8 cm long) about 1,325,600 eggs. The relationship between the number of spawned eggs and length was also curvilinear (see paper in this proceedings by Everson). All three species appeared to be partial spawners, but the number of times a fish spawned in a season was not determined (see paper in this proceedings by Kikkawa and Everson).

Feedings Habits

Studies of stomach contents and spew samples of hapuupuu, kahala, and pig ulua have been completed (see papers in this proceedings by Seki on hapuupuu and trevally; see paper in this proceedings by Humphreys and Kramer). Humpreys and Kramer found that the kahala could be separated into two size groups on the basis of their diet: small (<9 kg) and large (>9 kg). They also separated the prey into three general groups: bottom-associated prey, water column-associated prey, and prey that occupied both habitats. For small kahala from the NWHI, 83.8 percent of the stomach contents consisted of bottom-associated prey, 10.7 percent of water column organisms, and 5.5 percent of prey that occupied both habitats. On the other hand, large kahala preyed more heavily on water column organisms (38.1 percent); bottom-associated organisms comprised 58.0 percent of the prey and organisms associated with both the bottom and water column accounted for 3.9 percent. By volume, the content of small kahala stomachs contained 66.3 percent fish, 31.1 percent cephalopods, and 2.6 percent crustaceans. The content of large kahala stomachs differed by containing 96.2 percent fish, 3.1 percent cephalopods, and 0.7 percent crustaceans. Seki (see papers in this proceedings on hapuupuu and trevally) described both hapuupuu and pig ulua as carnivorous, opportunistic bottom feeders. The hapuupuu fed primarily on fish (76.1 percent) and also consumed some crustaceans (14.6 percent) and molluscs (8.3 percent) (by volume). It appeared to prefer pandalid shrimps which accounted for 64.4 percent of the food items by number but only 7.2 percent by volume. The pig ulua's diet was composed of 64.2 percent fish, 9.4 percent molluscs, 4.3 percent crustaceans, and 21.2 percent rubble and unidentified remains. The stomach contents of ehu were also examined, but not analyzed and the ehu has been described as a carnivorous bottom feeder (M.R. Seki, 1983: personal communication). Spew samples of opakapaka were found to consist of fish, crustaceans, molluscs, and chordates (S. Ralston, 1983: personal communications).

Ehu, hapuupuu, kahala, opakapaka, and pig ulua all had a number of bottom-associated diet items in common, but, except for ehu, each also had preference for a unique prey item. Hapuupuu ate a large number of small crustaceans (see paper in this proceedings by Seki on hapuupuu). Large kahala had a preference for Decapterus, a benthopelagic fish (see paper in this proceedings by Humphreys and Kramer). Opakapaka spew samples uniquely consisted of 42.2 percent by volume of Pyrosoma sp. (S. Ralston, 1983: personal communication), pelagic tunicates (Kami, 1973), and other chordates. The pig ulua's diet contained a high proportion of rubble (21.2 percent by volume) (see paper in this proceedings by Seki on trevally). No unique preferred item was noticed for ehu perhaps because of the small number of spew samples available. These five species appeared to compete for food at least part of the time.

Ciguatoxin Studies

Preliminary progress reports on ciguatoxin in fishes from the NWHI have been published (Ito and Uchida, 1980; Uchida et al., 1979, 1981). Toxicity level is believed to be related to fish size. In their preliminary report, Ito and Uchida (1980) reported a low but significant correlation exists between toxicity level and fish size. This relationship, however, is still under review (B.M. Ito, 1983: personal communication).

Humphreys and Kramer (see paper in this proceedings) compared the diets of kahala which had high radioimmunoassay counts indicating possible presence of ciguatoxin with the diets of nontoxic kahala. Overall diets were quite similar. However, differences between diets of small kahala (<9 kg) and large kahala (>9 kg) were found. Humphreys and Kramer hypothesized that small kahala, which feed on benthic organisms, pick up ciguatoxin in their diet and that large kahala, which feed primarily on pelagic _Decapterus_, contain accumulated toxin from an earlier benthic feeding phase.

Kikkawa and Everson (see paper in this proceedings) examined the occurrence of ciguatoxin in kahala in relation to the reproductive cycle and found no correlation.

CONCLUSIONS

The relative abundance and species composition of bottomfishes varied considerably throughout the NWHI. Most noteworthy was the dominance of opakapaka at Necker bank, French Frigate Shoals, and Brooks Banks, and of ehu west of Lisianski bank.

Members of the three families of bottomfishes studied spawn at different times, i.e., the grouper in winter, carangids in spring and early summer, and the snappers in August. Five species whose stomach contents and spews were examined all fed on an assortment of bottom-associated organisms, which suggested some degree of competition for prey. On the other hand, four species also fed on unique items, indicating niche sepration occurs for at least several species.

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Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*

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Summary. 1. Yellowfin tuna, *Thunnus albacares*, were trained individually to discriminate between two Earth-strength magnetic fields by differential reinforcement of a swimming response.

2. Seven subjects, of which two were trained with a double blind procedure designed to control for the possibility of cues from the experimenter, learned to discriminate between ambient and altered fields (Figs. 1–3).

3. Two additional fish trained with the same double blind procedure failed to discriminate between two magnetic fields in which the gradients of intensity were equal and opposite (Fig. 4).

4. The results suggest that the responses to magnetic fields by yellowfin tuna are neurally mediated and that magnetic field detection by this species can be analyzed by the same means as other sensory modalities.

Introduction

Classical and instrumental conditioning techniques often have failed to demonstrate responses by animals to magnetic fields (Ossenkopp and Barbeito 1978). For example, Reille (1968) reported successful heart rate conditioning to magnetic field stimuli in homing pigeons. However, Kreithen and Keeton (1974) and Beaugrand (1976) were unable to repeat this result. Homing pigeons showed statistically significant responses to magnetic fields when they fluttered in a flight tunnel before entering one or the other of two goal boxes in a choice conditioning procedure (Bookman 1977). However, an attempt to replicate this experiment failed (C. Walcott, Cornell University, Ithaca, New York, personal communication, 1982) and starlings failed to discriminate between two magnetic fields under similar conditions (Griffin 1982). In contrast, Phillips (1977) and Kalmijn (1978) were able to demonstrate conditioned responses to magnetic fields using salamanders and rays in choice procedures. Thus, despite conflicting results, there is evidence that animals can be trained to discriminate magnetic field stimuli. However, a wide range of techniques for demonstration and analysis of magnetic field detection by animals has been neither developed nor applied. Here I report training yellowfin tuna, *Thunnus albacares*, to distinguish between two different Earth-strength magnetic fields by requiring the fish to produce a single response and then manipulating the consequences of that response. Results obtained using this unitary discriminative training procedure permit inferences concerning the mechanism of magnetic field detection by these fish.

I tested juvenile yellowfin tuna for unconditioned responses to novel magnetic field stimuli and obtained results suggesting that this species might respond to magnetic fields in conditioning experiments. Fish were trained individually to swim through a narrow tunnel (60 × 30 cm) between two experimental tanks and reinforced according to a randomized schedule that provided the fish with a food reward on average once every five responses. The fish swam through the tunnel at a steady rate during training sessions held once daily. Swimming through a magnetic field anomaly induced momentarily within the tunnel caused the fish to delay returning through the tunnel even though the anomaly was removed before the fish could have responded again. The delay in response

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Abbreviation: *ITI* intertrial interval

*Present address: Southwest Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California 93028, USA caused by subsequent presentations of the anomaly decreased rapidly for all but one fish tested, suggesting that at first the fish were disturbed by the stimulus but that they later paid no attention to it.

The nature of magnetic fields, which are pervasive stimuli that can only be presented one at a time, influenced my choice of conditioning procedure. Discrimination training experiments in which subjects are presented with a choice of responses contingent upon such singly presented stimuli are very difficult discrimination problems and will frequently fail even with well understood, salient stimuli (Mackintosh 1974; Bitterman 1979). Consequently, I elected not to use a choice procedure for discrimination testing. Instead, I used a unitary discrimination training technique, known as a discrete-trials/fixed-interval training procedure (Woodard and Bitterman 1974), in which subjects could produce a single response repeatedly during trials of fixed duration but not during an interval which separated the trials. Rate of production of the response during trials provided a sensitive measure of discrimination of the stimuli by the fish.

The magnetic fields used in these experiments provided changes in angle of inclination, magnetic field intensity, and the gradients in inclination and intensity of the magnetic field. The fish could conceivably monitor any or all of the varying features to make the discrimination. The unitary procedure and the discriminative stimuli used in these experiments therefore provided as general a pair of stimuli as possible for the fish to distinguish in as simple a testing procedure as I could devise.

Materials and methods

Experimental facilities, apparatus, and animals. These experiments were conducted at the Kewalo Research Facility of the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service. Experimental tanks used were constructed of fiberglass or plywood and were 6 m in diameter by 0.75–1.0 m in depth. The absence of metal prevented distortion of the magnetic fields in the tanks arising from the tank construction. A direct current passed through 100 turns of No. 18 AWG magnet wire wrapped around the wall of each tank induced vertical magnetic fields in the tanks. The artificial fields were non-uniform, adding from 10 microTesla (μT; 10 μT = 0.1 Gauss) in the center to 50 μT at the edge of the tanks to the uniform Hawaiian field (inclination 38°; declination 11°30′ E; total intensity measured in the tanks with a Develco[1] 3-axis fluxgate magnetometer = approximately 30 μT).

Experiments were run from control rooms that were physically isolated from the tanks. Mechanical and electrical linkages in the control rooms operated the response apparatus and feeders, and direct current power suppliers generated the altered magnetic fields used in the experiments. The fish were observed through small viewing ports and their responses recorded manually.

Fish used in the experiments were juvenile yellowfin tuna (40–50 cm fork length) held in outdoor holding tanks at the Kewalo Research Facility. For testing, fish were moved individually to one of the experimental tanks and allowed to adapt to the new situation for 2 days. During this time they were fed from a feeder which dropped food into the water approximately 1 m from the edge of the experimental tank (Jemison et al. 1982).

Discriminative training procedure. After the adaptation period, the experiments were conducted in two stages. The fish were first pre-trained to produce a conditioned response at a steady rate in anticipation of a food reward. In the second, discrimination training stage, this response was reinforced with food or not reinforced depending on the magnetic field present in the tank. Discrimination was detected by comparing the rates at which the response was produced in the presence of the two stimuli. Training sessions lasted 1–2 h, were held once daily between 0800 and 1600, and took place at approximately the same time each day for each fish. The 60- × 30-cm pipe frame was lowered into the water and the fish enticed through it using a bait hanging in front of the opening. The bait was removed as the fish struck at it and became committed to swimming through the frame. A piece of food (cut smelt) was then delivered to the fish to reinforce the response. By the end of the first session, the fish usually began to swim through the frame spontaneously and all fish responded freely after the second training session.

Each subsequent session consisted of 15 30-s trial periods during each of which the pipe frame was lowered into the tank and the fish allowed to respond freely. The first response after 30 s brought food from the feeder and the frame was retracted for a variable inter-trial interval (ITI), which averaged 3 min in this pre-training period.

To ensure that the fish only gained experience from receiving food in association with the correct stimulus, the magnetic field that was later to become the reinforced stimulus (designated S+) was presented simultaneously with the pipe frame during pre-training. That is, if the altered field was to become S+ during discrimination training, the field was switched on at the same time as the pipe frame was lowered into the tank and switched off at the end of the trial when the frame was removed. If the altered field was later to become the non-reinforced stimulus (designated S−), the fish gained no experience with that field at any stage during the pre-training period.

After 2 days of pre-training, discrimination training began. In this training, each trial began with simultaneous presentation of the pipe frame and either the reinforced or non-reinforced stimulus. All responses by the fish in the 30-s trial were counted. On S+ trials the fish was given a piece of food at the first response after 30 s and the trials were terminated. On S− trials a 10-s penalty timer started at the end of the 30-s period. If the fish responded before the 10 s had elapsed, the timer was reset. The timer was reset by each subsequent response until either the fish failed to respond for 10 s or until a total of 30 s of penalty time had elapsed. Response to S− was thus penalized by extending the trial without any possibility of the fish obtaining food for producing the response (Woodard and Bitterman 1974). After the trials were terminated, the pipe frame was retracted for a variable ITI (mean 90 s) after which another trial sequence began. The upper limit of 30 s of accumulated penalty time per trial was initially established because the fish often jumped out of the experimental tanks when the penalty time was longer during pilot experiments used to develop the procedure. In subsequent experiments (see below), the maximum penalty time allowed was increased without causing the fish to jump out of the experimental tanks. An important feature of the discrete-trials/fixed-interval training method is that the rate of response to the stimuli is measured during a trial period in which the fish receives no reinforcement for responding. Therefore, the possibility that the reinforcement itself might provide a cue is excluded.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

The fish were trained in 30-trial sessions held once daily. In each session, S+ or S− were presented equally often in a quasi-random order with no more than three S+ or S− trials in succession. Reduction of the mean ITI from 3 min to 90 s resulted in the fish receiving about the same number of reinforcements per unit time as in the pre-training. To ensure that any difference in response to the two magnetic field stimuli was not due to some differential effect of the fields on the general behaviour of the fish (as, for example, disorientation caused by the altered field), testing was balanced by training some fish with the normal Hawaiian field as S+ and others with the altered field as S+.

In subsequent experiments, designed to exclude possible observer-related cues, fish were tested using double blind procedures. The penalty timer was set at 15 s and the total allowable penalty time was up to 90 s. In the double blind procedure, two people working in different rooms controlled different components of the experiment. Communication was by signal light and a simple code. The first person (the field controller) timed the trials and presented the discriminative stimuli. The second person (the apparatus controller) was directed by the first to raise and lower the pipe frame and, at the end of each trial, whether or not to deliver food. The apparatus controller recorded the responses made by the fish during the trials and signaled the field controller when each command had been executed. The apparatus controller was given no knowledge of the magnetic field conditions or which was S+ or S−, whereas the field controller had no knowledge of events under the control of the apparatus controller.

A second manipulation of the experimental procedure involved use of a different pair of discriminative stimuli in the same double blind procedure. In the original procedure, the normal Hawaiian magnetic field was used as one of the discriminative stimuli. This field was present at all times outside the experimental training sessions and so may have adversely influenced the performance of the fish during discrimination training in which it was S+. An attempt was therefore made to use as discriminative stimuli two magnetic fields that could only be detected during the experiments. A second altered field was generated by reversing the direction of the current through the coil around one of the experimental tanks. The fields added to the background field were of equal intensity but were opposite in their inclination and in their gradients of intensity and inclination. As a result, total intensity and inclination at any point in the tank differed between the two experimental fields. The gradients of intensity in the tank were the same, although of opposite sign.

Results

Mean response rate data for sequential blocks of five pre-training, S+, and S− trials were used in graphical presentation and statistical analysis of results of the experiments. In the pre-training period the fish established variable baseline response rates. At first the fish responded at low rates but over the course of two training sessions their response rates increased considerably (Figs. 1–4). Rates produced by individual fish usually appeared to stabilize after two pre-training sessions, although this is not reflected in the pooled data. Differences among the rates produced by individual fish seemed to be due primarily to the different sizes of the fish relative to the opening in the pipe frame and the different approaches to the frame employed by each fish. The smallest fish were usually more active and able to turn more rapidly near the pipe frame than the larger fish used. Fish that swam in circles and approached the frame predominantly from one direction established lower rates of response than fish that approached it freely from both sides in figure-eight patterns centered on the frame.

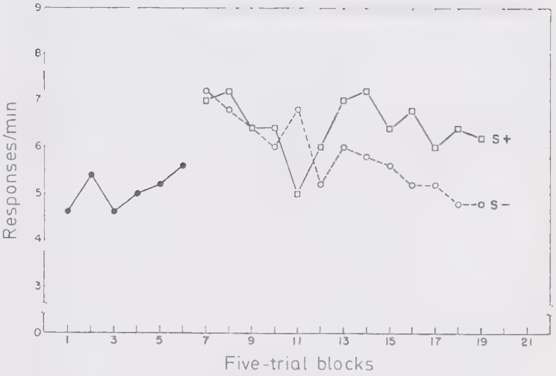

Fig. 1. Response acquisition and discrimination learning in five yellowfin tuna. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S− (open circles) (blocks 7–19) trials for all fish tested

For five fish used in the first series of experiments, discrimination between the two magnetic fields became evident after two training sessions. On the first 2 days (blocks 7–12 in Figs. 1 and 2), response rates to the two stimuli fluctuated about each other. By the third day, all fish produced higher rates of response to the reinforced than to the non-reinforced stimulus and continued to do so for the remainder of the experiments. Comparison of response rates between paired five-trial blocks demonstrated significant differences in response to S+ and S− by all except one of the fish (Wilcoxon rank sum, $P<0.01$ for fish 1 and 3, $P<0.05$ for fish 2 and 5 in Fig. 2). However, the positive ranks for this fish (Fish 4 in Fig. 2) were all contained in the last 8 five-trial blocks, suggesting that the response of the fish to S+ and S− changed during the course of the experiment.

All fish completed at least 13 five-trial blocks

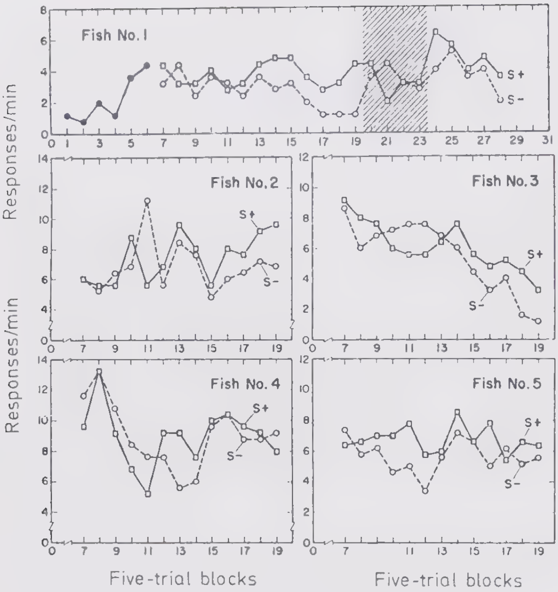

Fig. 2. Individual results of dicsrimination training for the same five fish shown in Fig. 1. Each point is the mean of five pre-training (closed circles, blocks 1-6, shown for Fish 1 only), or S+ (open squares), and S− (open circles) trials. Shaded area indicates control trials (in which the connection between the coil and the power supply was broken) for Fish 1

Table 1. Magnetic field discrimination learning. Results of analysis of variance comparing S+ and S− response rates for five yellowfin tuna. *b* blocks; *s* stimuli; *j* subjects; *t* trials

Source	d.f.	Mean square	*F*	Probability
Total	649			
Blocks	4			
s	1	13.8846	8.4543	0.0438
js	4	1.6423		
b	12	3.3087	0.6881	0.7544
jb	48	4.8084		
sb	12	3.4046	2.8776	0.0046
jsb	48	1.1831		
t	4	1.3054	1.1538	0.3675
jt	16	1.1313		
st	4	2.6731	2.2011	0.1151
jst	16	1.2144		
bt	48	1.3379	0.9855	0.5072
jbt	192	1.3576		
sbt	48	1.4722	0.9595	0.5534
jsbt	192	1.5344		

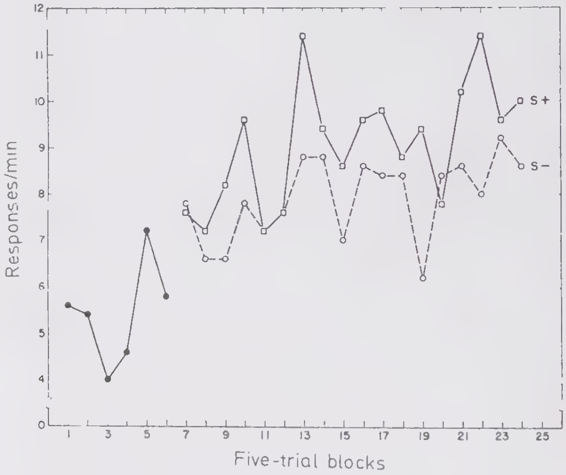

Fig. 3. Response acquisition and magnetic field discrimination learning in two yellowfin tuna tested in double blind experiments. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S− (open circles) (blocks 7–24) trials

of discrimination training (blocks 7–19 in Fig. 1). An analysis of variance (ANOVA) demonstrated a significant difference in overall mean response rates to S+ and S− during discrimination training $F_{(1,4)\ \mathrm{stimuli}} = 8.4543$, $P = 0.0438$; Table 1). Analysis of interactions within the ANOVA demonstrated only one significant source of variance, the stimuli by blocks or learning effect interaction $F_{(12,48)\ \mathrm{stimuli\ by\ blocks}} = 2.8776$, $P = 0.0046$). This result indicates that response rates to the two stimuli changed differentially with time as the fish learned to discriminate between the stimuli during the experiments.

To test whether the fish were responding to possible equipment or observer-related cues, control trials were conducted with one fish. One of the wires connecting the power supply to the coil around the tank was disconnected and all procedures followed as before. The response rates during reinforced and non-reinforced trials fluctuated about each other during this period (Fish 1 in Fig. 2). When the circuit between the power supply and the coil was reestablished, the fish again produced higher response rates to the reinforced than to the non-reinforced stimulus (Fig. 2). However, the differences between response rates was less than immediately before the control trials were conducted.

The two fish tested had little difficulty in learning the discrimination in spite of the extensive precautions taken to remove observer-related cues in the first set of double blind experiments. In addition, discrimination became evident considerably earlier, by the end of the first 30-trial session, than in the previous experiments (Fig. 3). This improvement in response is attributed to the greater pen-

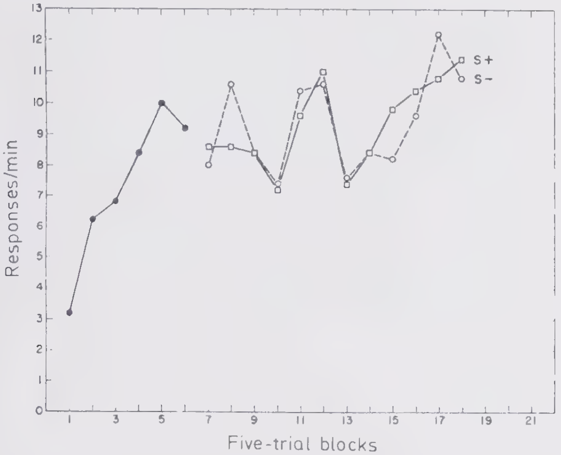

Fig. 4. Response acquisition and discrimination performance in two yellowfin tuna tested using the same double blind procedures as in Fig. 3. Magnetic fields used in these experiments were generated by currents of equal magnitude but reversed polarity. Each point is the mean of five pre-training (closed circles, blocks 1–6) or S+ (open squares) and S− (open circles) (blocks 7–18) trials

alty the fish incurred for continued response to S− in these experiments.

In the second set of double blind experiments, an attempt was made to improve discrimination by providing stimuli that were not present in the tank at any time other than during the training. As noted above, the two fields used in these experiments were produced by currents of equal magnitude but reversed polarity passing through the coil. At no stage of training did either of the two fish tested show evidence of discrimination (Fig. 4). It seems unlikely that two fish would fail to respond in this procedure when seven had previously done so in experiments that were either identical or differed only in the amount of penalty time allowed. It therefore appears that the fish could not distinguish between the two fields used in these experiments whereas they could distinguish between the fields used in all the previous experiments.

Discussion

The discrimination training reported here demonstrated reproducible conditioned responses to Earth-strength magnetic field stimuli in experiments employing a new procedure and a new species. The discrete-trials/fixed-interval training procedure had several advantages for demonstrating magnetic field discrimination in the yellowfin tuna. Requiring multiple responses sharpens discrimination (Bitterman 1979), and rate of response is an effective measure of discrimination because it accommodates variability in behaviour but can vary widely and rapidly in response to changes in experimental conditions (Kling 1971). In addition, discrimination between singly presented stimuli is generally more easily demonstrated with unitary than with choice procedures (Bitterman 1979; Mackintosh 1974).

Variation in control of the conditioned behaviour by the discriminative stimuli was evident in the control experiment. Only the background Hawaiian magnetic field was present in the tank during the control trials, and this field was associated with both reinforcement and non-reinforcement. When the two discriminative stimuli were again presented the difference between response rates was smaller than before the control trials were conducted (Fig. 2), suggesting that experience gained during the control trials modified subsequent responding by the fish.

Despite its success the unitary procedure as used in these experiments does have clear limitations. The use of a 'whole body' response caused the rates of response produced by the fish to be low compared with rates obtained using conditioned responses such as hitting a target (Woodard and Bitterman 1974). Consequently, the scope for change in response rate was low and the variability in responding high compared with the performance ceiling. The ability of tunas to maintain high swimming speeds was probably an important factor in overcoming this difficulty. The wide scope for changes in the swimming activity of the fish increased the sensitivity of the conditioning technique by allowing a wider scope for change in response rates during the experiments than might have been obtained with other, less active fishes.

Although they have proven useful in using the discrete-trials/fixed-interval procedure to demonstrate conditioned responses to magnetic fields, yellowfin and other tunas are probably not ideal subjects for magnetic field conditioning studies. The size of the fish and the tanks required to house them make it difficult to obtain good control of the experimental environment and stimulus. A further difficulty in working with tunas is that the fish are under stress in captivity and are difficult to maintain alone in experimental tanks. More specific experiments, for example those that require handling of the fish for impairment of sensory function, would be impossible with tunas because of their fragility (Queenth and Brill 1983). For these reasons, other species may be found to be more suitable for magnetic field conditioning studies as the techniques are developed further.

It is not known which features of the magnetic fields the fish used to make the discrimination. The first two groups of experiments used magnetic fields varying in their angles of inclination, total intensity, and the gradients in these two features in the experimental environment. The fields used in the third group of experiments differed in total intensity and inclination at any point in the experimental tank. However, the gradients in intensity in the tank were equal (high near the edge and low near the center of the tank) although opposite in sign (increasing and decreasing to 0 from the edge to the center of the tank). Two fish were completely unable to discriminate between these two magnetic fields (Fig. 4) when seven others tested under the same conditions but with different fields showed good discrimination (Figs. 1–3). Although other interpretations are possible, the very large differences in intensity gradients between the normal and altered fields probably made discrimination easier for fish presented with these fields as discriminative stimuli.

The experiments permit the inference that magnetoreception by yellowfin tuna is neurally mediated. Training different fish with either the altered or the normal field as S+ and the highly significant learning effect interaction in the analysis of variance exlude the explanation that the differences in response to S+ and S− merely resulted from some differential physiological effect of the fields on the behaviour of the fish. In addition, the rapidity with which the fish were able to make the discriminatory decision in each trial suggests that magnetoreception occurs through neural rather than non-neural processes.

A second inference that can be made from these experiments concerns the magnetic field transduction mechanism. The suggestion that movement is required for use of magnetic field stimuli (Kreithen and Keeton 1974; Bookman 1977) is compatible with the hypothesis of magnetoreception by electrical induction (Kalmijn 1974; Jungerman and Rosenblum 1980). However, yellowfin tuna do not possess the large ampullary canals necessary for ampullary electroreception in salt water. In addition, I saw no evidence that the induced electrical fields associated with the presence or absence of water currents in the experimental tanks, or the rate at which the magnetic field was changed, affected discrimination by the fish. Magnetoreception might occur by induction in the labyrinth organ of the inner ear of the yellowfin tuna, although the fish cannot make the rotatory movements of the head that Jungerman and Rosenblum (1980) consider necessary for this mechanism. Although magnetoreception based on electrical induction mechanisms cannot be excluded, these observations suggest it is unlikely that yellowfin tuna detect magnetic fields by electrical induction.

My results are also compatible with the magnetite-based magnetoreception hypothesis suggested to explain responses to magnetic fields in honeybees and homing pigeons (Yorke 1979, 1981; Kirschvink and Gould 1981). With my colleagues, I have reported elsewhere that the yellowfin tuna produce single-domain crystals of magnetite in tissue found within the dermethmoid bone of the skull (Walker et al. 1984). These particles could provide an ideal physical basis for the behavioural responses to magnetic fields by yellowfin tuna reported in this paper. However, specific tests will be necessary to determine whether magnetoreception by yellowfin tuna has a ferromagnetic transduction mechanism.

In summary, these behavioural studies demonstrated reproducible responses to magnetic fields in yellowfin tuna. The success of the experiments is attributed to use of a species that is very likely to benefit from possession of a magnetic sense (Tesch 1980) using very different magnetic field stimuli in an appropriate testing procedure. The results suggest that magnetic field detection is neurally mediated and can be analyzed by the same means as other sensory modalities. Future work must seek to repeat these results, develop tests for responses to individual components of the geomagnetic field, and begin analyzing the magnetic field transduction mechanism.

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MAGNETIC SENSITIVITY AND ITS POSSIBLE PHYSICAL BASIS IN THE YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

Many animals are known to orient to magnetic fields. However, two central problems in the study of magnetic sensitivity have been the almost complete failure of magnetic field conditioning experiments and the lack of evidence for a feasible transduction mechanism. In the studies reported here yellowfin tuna learned to discriminate between two Earth-strength magnetic fields in a discrete-trials/fixed-interval conditioning procedure. Magnetometry experiments, diffraction spectra and electron microscope analyses demonstrated single-domain crystals of the ferromagnetic mineral magnetite in the head of this species. The crystals are concentrated in tissue contained within a sinus formed by the ethmoid bones of the skull. Theoretical analyses show that the crystals would be suitable for use in magnetoreception if linked to the nervous system. The physical properties of the crystals would determine the operation of magnetoreceptor organelles and constrain the capacities of the magnetic sense. Tests of these constraints in appropriately designed conditioning experiments will provide powerful tests of the ferromagnetic magnetoreception hypothesis.

INTRODUCTION

For pelagic fishes migration represents a substantial investment of energy (Sharp and Dotson 1977). These energetic costs imply intense selection on the sensory mechanisms that guide migration. With the exception of the upstream migration of salmon (Hasler et al. 1978) the known capacities of the sensory systems of fishes are not sufficient to explain their navigational achievements (Tesch 1980). We must therefore either reexamine the capacities of the known sensory systems or attempt to find new systems that could provide fish with the necessary sensory abilities (Kreithen 1978). This paper takes the second of these approaches, investigating the responses of yellowfin tuna to magnetic fields and a possible transduction mechanism for the magnetic sense of this and other migratory fishes.

Many animals from different taxa are known to respond to one or more features of the geomagnetic field (Keeton 1971, 1972; Wiltschko 1972; Walcott and Green 1974; Lindauer and Martin 1972; Martin and Lindauer 1977; Quinn 1980; Wiltschko et al. 1981). These responses fall into two general categories--responses to magnetic field direction and to magnetic field intensity. Although the experimental results are repeatable, they are primarily based on unconditioned responses and tell us little about the sensory mechanism and its capacities.

The central problems in the study of magnetic sensitivity in animals have been the almost universal failure of magnetic field conditioning experiments and the lack of evidence for any of the hypothesized magnetic field transduction mechanisms. Conditioning experiments have either failed or been unrepeatable (Reille 1968; Kreithen and Keeton 1974; Beaugrand 1976; Bookman 1977, 1978). Where conditioning was obtained (Kalmijn 1978) subsequent psychophysical analyses of the capacities of the sense were either not done or not reported. Numerous magnetic field transduction mechanisms have been suggested (e.g., Kalmijn 1974; Leask 1977; Jungerman and Rosenblum 1980), but many are unacceptable because they do not explain the general responses to magnetic fields by animals or because magnetoreception is known to occur when the special conditions required by the hypotheses are not met (e.g., Phillips and Adler 1978; Quinn et al. 1981).

The hypothesis that the basis of the magnetic sense is single-domain crystals of magnetite produced by animals has attracted much attention in recent years (Gould et al. 1978; Walcott et al. 1979; J.L. Kirschvink, M.M. Walker, A.E. Dizon, and K.A. Peterson unpublished). This hypothesis is appealing because it can explain the general responses of animals to magnetic fields (Yorke 1979, 1981; Kirschvink and Gould 1981) and lends itself to behavioral testing (Kalmijn 1981; Kirschvink 1981). It also provides us with the basis for a search for receptors which could mediate the behavioral responses.

In this paper I report the use of an orthodox behavioral conditioning paradigm (Woodard and Bitterman 1974) to train yellowfin tuna to discriminate between two different earth-strength magnetic fields. I also demonstrate the presence of single-domain magnetite crystals in the skull of this species. Based on the theoretical analysis of J.L. Kirschvink and M.M. Walker (unpublished) I then propose behavioral experiments to test for constraints on magnetoreceptor operation resulting from the physical properties of the magnetite crystals. Pending demonstration of a functional link between the crystals and the nervous system these experiments will provide the best test of the ferromagnetic magnetoreception hypothesis.

CONDITIONING EXPERIMENTS

Different magnetic field stimuli can be delivered only successively and not simultaneously. Therefore, in magnetic field conditioning experiments the subject cannot make a simultaneous comparison of stimuli. This limits the choice of conditioning procedures to those which are effective using singly presented discriminative stimuli. The approach I chose was to define a single response, to reward that response under one set of magnetic field conditions and not under another, and to compare the readiness with which the response was expressed under the two conditions (Bitterman 1966). The measure of behavior compared between the stimulus conditions was the rate of performance of a conditioned response. The primary advantage of rate as a measure of discrimination is its sensitivity; it can vary widely and rapidly in response to changes in experimental conditions and can accommodate short-term variability in behavior (Kling 1971). This approach seemed likely to test efficiently the ability of yellowfin tuna to discriminate between different magnetic fields.

These experiments were conducted at the Kewalo Research Facility of the National Marine Fisheries Service, Honolulu Laboratory. The fish used were juvenile yellowfin tuna (40-50 cm fork length) tested individually in one of two cylindrical test tanks (6 m diameter, 0.75 m depth). The experimental tanks contained no metal and each had 100 turns of number 18 AWG copper wire wrapped around its perimeter. A 1-ampere direct current passing through these wires added a vertical magnetic field to the background field. This field was nonuniform, adding from 10 microTesla (μT) in the center to 50 μT at the edge of each tank. The response apparatus was a 60- x 30-cm pipe frame lowered into the tank during trial periods and retracted during intertrial periods. The frame, the magnetic field and a semi-automatic feeder mounted at the side of the tank (Jemison et al. 1982) were operated by mechanical and electrical linkages from the experimental control room. The control room was physically isolated from the experimental tank and was darkened during experiments. The fish were observed through small viewing ports and their responses recorded manually.

The differences between the two magnetic fields used in the discrimination experiments were as follows. The local Hawaiian field was uniform throughout the tanks. That is, inclination, declination and total field intensity were the same at any point in the area occupied by the fish. The altered field introduced significant radially oriented gradients of both intensity and inclination within the tanks. These experiments therefore provided the fish with two very different magnetic fields as discriminative stimuli. The fish could conceivably monitor differences in magnetic field inclination, intensity or the gradients in these two parameters to make the discrimination.

After being allowed to acclimate to the experimental tanks fish were trained to swim through the pipe frame for a food reward (a piece of cut smelt, Osmeridae) delivered from the feeder. In discrimination testing a trial began with simultaneous presentation of the pipe frame and either the positively (S+) or negatively (S-) reinforced stimulus. All responses by the fish within a 30-second trial period were counted. In S+ trials the fish was rewarded with a piece of food following the first response after 30 seconds. In S- trials a 10-second penalty timer started at the end of the trial period. The timer was reset by each subsequent response by the fish until either the penalty time elapsed or a total of 30 seconds of penalty had accumulated. Response to S- was thus penalized by extending the trial without any possibility of the fish obtaining food. After reinforcement had been given the pipe frame was retracted for a variable intertrial interval (mean 90 seconds) after which another trial sequence began.

The fish were given 30 trial training sessions once daily. In any trial session the S+ and S- were presented 15 times, with no more than three S+ or S- trials in succession. Testing was balanced by training two fish with the normal Hawaiian field and two with the altered field as S+. Statistical treatment of the data was by analysis of variance.

Discrimination between the two magnetic field conditions occurred after two 30 trial sessions (Fig. 1). During the first two sessions there was no separation of response rates but from the third day all four fish maintained different rates of responding during S+ and S- trials. An analysis of variance comparing S+ and S- response rates before and after 60 trials for all four fish yielded an $F(1,3)$ stimuli 7.61, $P = 0.07$, and an $F(1,3)$ stimuli by blocks = 102.55, $P = 0.002$. All other comparisons within the analysis did not approach significance.

Control trials were performed with one fish by interrupting the current to the coil; normal procedures were then followed. The

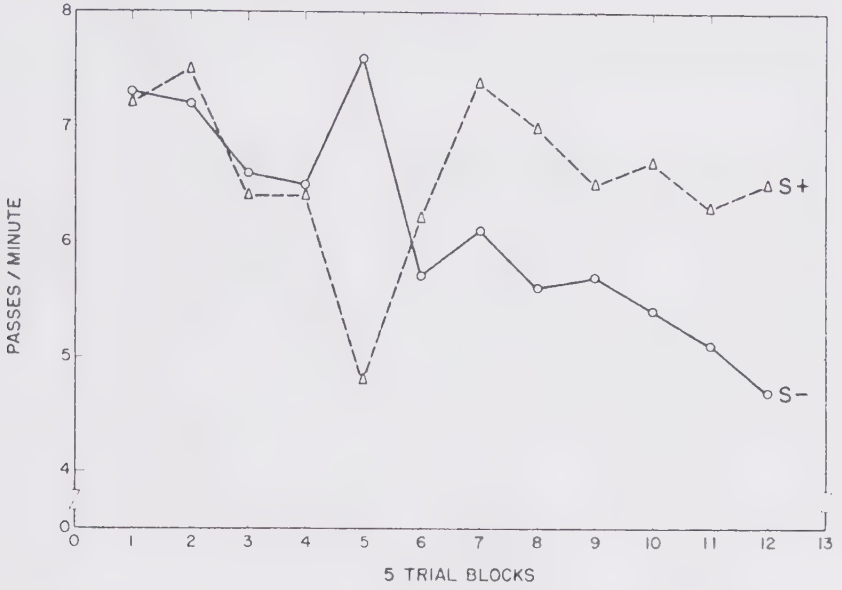

Figure 1. Magnetic field discrimination learning in yellowfin tuna. Each point is the average of five S+ or S− trials for the four fish tested. (Walker et al. 1982; (C) 1982 IEEE.)

response rates during S+ and S− trials fluctuated randomly during this period (Fig. 2). When the power supply was reconnected to the coil the fish was again able to make the discrimination, although

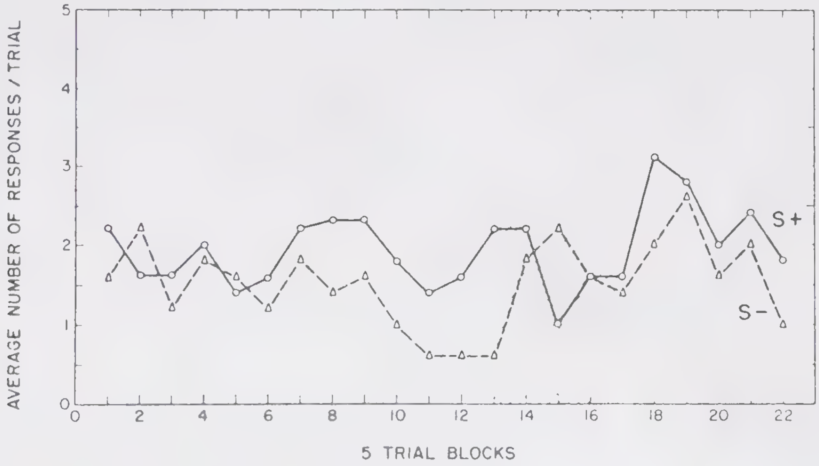

Figure 2. Magnetic field discrimination learning in yellowfin tuna. Control tests shaded. (Walker et al. 1982; (C) 1982 IEEE.)

less strongly than before the control trials were conducted. Evidently the magnetic fields used in the experiment were necessary for anticipation of positive and negative reinforcement by the fish.

These experiments demonstrate the ability of yellowfin tuna to discriminate between different earth-strength magnetic fields. Although the discrimination is consistent in all individuals it is consistently weak. This results from limitations imposed by the fish themselves. Tunas swim continuously and can only be conditioned to produce responses involving movement of their whole body (Iversen 1967; Nakamura 1968). The fish therefore did not attain high rates of performance of the response used to compensate for this limitation. Consequently the scope for change in response rate was low and the variation in responding was high compared to the mean response rate. The upper limit of 30 seconds of penalty time was established because some fish jumped out of the experimental tanks during development of the procedure. This made the "cost" of response to S- low so that the penalty time could only be expected to suppress S- responding weakly. That the fish were able to discriminate between the two fields at all, given these limitations on the procedure, suggests that their magnetic sense is well developed and underlines the sensitivity of response rate as a measure of discrimination.

The conditioning technique used here should be applicable to a range of studies on magnetic sensitivity. Other tunas (skipjack tuna, *Katsuwonus pelamis*, and kawakawa, *Euthynnus affinis*) have shown evidence of magnetic sensitivity in preliminary conditioning experiments (Walker unpublished data). These studies should be continued and extended to other species. The technique can also be used to test whether fishes possess a magnetic compass responding to magnetic field inclination or polarity. This can be achieved by testing for the ability of fish to discriminate between fields in which horizontal or vertical components of the field are reversed. A polarity sensitive compass should discriminate between fields with horizontal, but not vertical, components reversed. An axial or inclination sensitive compass should permit the fish to discriminate between fields with vertical, but not horizontal, components reversed (Wiltschko 1972).

The experiments carried out so far reveal nothing about the mechanism by which the tunas detect magnetic fields. I saw no evidence that the induced electrical fields associated with the presence or absence of water currents in the experimental tanks or the rate at which the magnetic field was changed affected discrimination by the fish. Similarly, Quinn et al. (1981) concluded that sockeye salmon fry and smolts must be able to detect magnetic fields in the absence of water flow in both fresh and salt water. From this behavioral evidence it seems unlikely that these teleost fishes detect magnetic fields by electrical induction in spite of the known electric field sensitivity of Atlantic salmon, *Salmo salar* (Rommel and McCleave 1973). It therefore seems important to identify and test other hypotheses for magnetic field transduction mechanisms in teleost fishes.

PHYSICAL BASIS FOR MAGNETIC FIELD TRANSDUCTION

Magnetometry Experiments

Magnetic material has been detected in a variety of domain states in tissues of a number of different animals (Gould et al. 1978; Walcott et al. 1979; Presti and Pettigrew 1980; Mather and Baker 1981; Zoeger et al. 1981; Jones and MacFadden 1982). In the yellowfin tuna I sought to distinguish magnetic material that might be used in magnetoreception from other deposits by identifying particles in a suitable domain state that could be consistently found in the same place in different individuals. All the tissues that could be identified and extracted from the body of the yellowfin tuna using glass microtome knives were tested for saturation isothermal remanent magnetization (sIRM) in a superconducting magnetometer. A feature of these studies is the small amounts of material involved and the ease with which contamination can influence the results. Procedures for avoiding entry of contaminants and tests for their presence in sample tissues have been developed and described in detail elsewhere (Kirschvink 1983).

There is a battery of paleomagnetic techniques available for the study of magnetic minerals. These techniques require some special adaptations for use in the study of biomagnetism. The magnetic fields associated with crystals of magnetic minerals in animals are very small and could not be detected in the presence of a background field. In a null field environment and at room temperature the crystal moments would be randomly oriented and not detectable. To detect the crystals it is necessary to freeze the sample tissue and prevent the orientation of the crystals from changing under the influence of thermal agitation (Kirschvink 1983). It is then possible to realign the moments of the crystals with a strong inducing magnetic field pulse (>0.3 T). The crystal moments then sum to produce the sIRM (also known as the moment of the sample) and become detectable in a superconducting magnetometer, if they are sufficiently concentrated in a tissue (1 100 nm crystal per 30,000 cells in a 9 mm^3 sample (Kirschvink 1983)).

A superconducting magnetometer detects weak magnetic fields in the samples and also magnetic field noise within the magnetometer itself. These measurements are combined to produce a signal to noise ratio for a tissue sample. Intensity of magnetization indicates the concentration of magnetic material within a sample and is estimated by dividing its moment by its volume (Kirschvink 1983). In this study to be considered magnetic a tissue had to show high values for both these measures compared to other tissues taken from the same fish.

Magnetic crystals tend to have their moments aligned in an "easy" direction, usually the long axis of the crystals (Kirschvink and Gould 1981). The microscopic coercivity of the crystals is the magnetic field required to cause their moments to reverse direction. This coercivity is dependent on the size, shape and domain state of the crystals. Progressive alternating field (AF) demagnetization of a magnetic sample subjects the aligned crystal moments to decaying sinusoidal magnetic fields oriented in one axis. The orientation of the moments of magnetic crystals with coercivities less than the maximum alternating field applied will be randomized by this procedure. The contribution of the randomized crystal moments to the IRM will thus be removed and can be detected in the magnetometer as a reduction in the moment of a sample. The size of the randomizing field required to decrease the IRM to half its saturation value gives an estimate of the median coercivity of the crystals present in a sample. From this we can determine the likely source of the sIRM and the size, shape and domain state of the magnetic crystals.

The magnetometry experiments demonstrated that magnetic material is concentrated only in the head of the yellowfin tuna. Eighteen samples of tissues and organs extracted from a representative fish were not magnetic. A few samples showed either high signal to noise

Table 1. Values of saturation isothermal remanent magnetization in various tissues of a representative yellowfin tuna. Signal-to-noise values are the ratio of the measured value of the tissue to the mean of the noise level before and after the sample was measured. (Walker et al. 1982; (C) 1982 IEEE.)

Tissue	Signal-to-noise ratio	Magnetic intensity (picoTesla)
Left pectoral fin	1.5	45.3
Peduncle tendon	2.5	35.8
Gill	4.6	20.3
Eye	10.1	4.1
Whole parethmoid	15.4	39.4
Left rear parethmoid	11.0	47.4
Right rear parethmoid	18.5	255.3

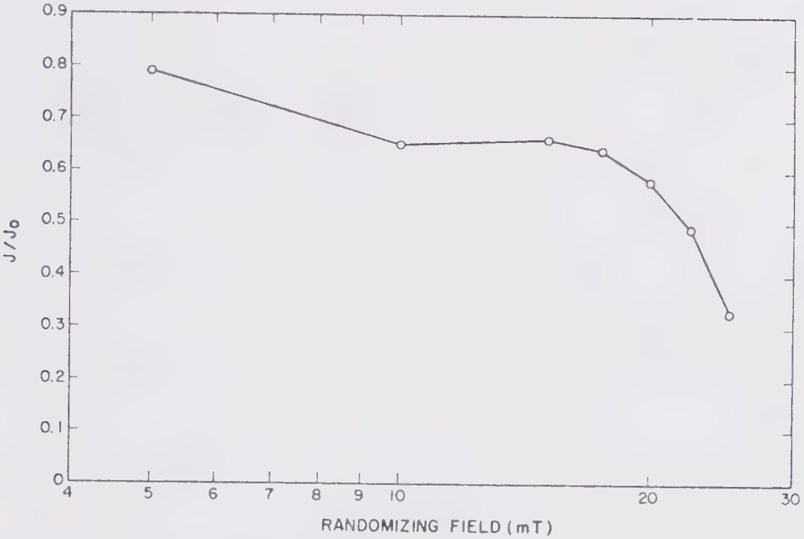

Figure 3. Progressive alternating field demagnetization of the ethmoids of three yellowfin tuna.

ratios or intensities of magnetization (Table 1). These I judged to be nonmagnetic and excluded from consideration. Only samples from the ethmoid bones of the fish's skull exhibited high values for both measures of magnetization (Table 1) in that and all other individuals tested. Progressive AF demagnetization of the ethmoid bones of three yellowfin tuna gave an estimate of median coercivity for the magnetic particles of 22.5 mT (Fig. 3). This is consistent with the presence of a dispersion of single-domain magnetite crystals with particle lengths and diameters of approximately 50 and 40 nm (McElhinny 1973). The narrow range of particle sizes is unlike the pattern observed for geologic and synthetic magnetite crystals, which commonly exhibit log-normal distributions (J.L. Kirschvink personal communication).

Identification of the Magnetic Material

Although the magnetometry experiments indicate that the ethmoids of the yellowfin tuna contain ferromagnetic particles they do not uniquely identify the mineral involved. Extraction of the crystals themselves is necessary to do this and to confirm the estimates of their size and shape. Using glass knives I removed the tissue from within the ethmoids of five yellowfin tuna, ground the tissue in a glass tissue grinder, extracted released fats with ether and digested the remaining cellular material in several changes of millipore-filtered 5% hypochlorite solution (commercial bleach). After centrifuging and washing the digested material small black aggregates of crystals could be attracted to a magnet held to the side of the test tube. These aggregates could then be pipetted onto slides for analyses of diffraction spectra. A brief digestion in buffered EDTA was necessary to obtain aggregates that could be dispersed completely by an alternating magnetic field after they were pipetted onto carbon-coated copper mesh grids. This made it possible to examine individual crystals in the transmission electron microscope (TEM).

X-ray diffraction of the magnetic aggregates extracted from the ethmoid tissue of the yellowfin tuna uniquely identified the crystals as magnetite. An electron microprobe analysis showed that the crystals contained no measurable titanium, manganese, nor chromium, indicating that the crystals were probably not of geologic origin. The crystals averaged 45 x 38 nm and appeared to be hexagonal in cross section. They are thus single-domains and conform to the sizes estimated from their coercivities. The nonoctahedral crystal habit adopted by these crystals in the yellowfin tuna distinguishes them from all geologic and synthetic magnetites. Thus we have evidence from a number of sources that the magnetite crystals found in the ethmoid tissue of the yellowfin tuna must have been produced by the fish themselves. The fish do this with close control over the size, shape and composition of the crystals. They therefore control the physical properties of the crystals and so control their operation in the hypothetical magnetoreceptors considered next.

THE FERROMAGNETIC MAGNETORECEPTION HYPOTHESIS

The basis for magnetite-based magnetoreception is the torque exerted on single-domain magnetite crystals by the geomagnetic field. This torque is described by the relation $\tau = \mu \times B$ where τ is the torque, μ is the moment of a magnetite crystal and B is the intensity of the external magnetic field. The torque will cause the crystals to align with the external field. At physiological temperatures in a live fish the crystals will be subject to thermal agitation, which will cause their vector direction to wander randomly about the applied field direction. The mean alignment of the crystals will be in the direction of the external field so that a compass receptor system needs only to monitor the orientation of up to 1,000 crystals or groups of crystals to detect magnetic field direction accurately (Yorke 1979). The variance of the orientation of the crystals about the external field will depend on its intensity (Kirschvink and Gould 1981; Yorke 1981). Monitoring the variance will thus provide the physical basis for a response to magnetic field intensity (Gould 1980, 1982; Moore 1980; Walcott 1980).

The above analysis yields three testable behavioral predictions (J.L. Kirschvink and M.M. Walker unpublished). The first is that the magnetic sense organ should be made up of separate, independent compass and intensity receptors with different magnetic moments. The second is that the accuracy of the compass response should be

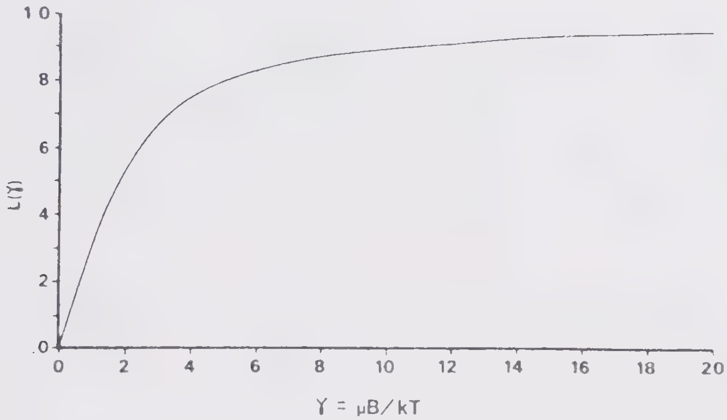

Figure 4. The Langevin function plotted against γ, the ratio of magnetic to thermal energies for single domain magnetite crystals. The accuracy of alignment of the crystals (L(γ)) increases rapidly up to γ values of about six and increases asymptotically thereafter. The accuracy of behavioral responses to magnetic field direction mediated by magnetite-based magnetoreceptors should at first increase rapidly with external field intensity. Beyond a certain point further increase in external field intensity should not lead to greater compass accuracy. (Modified from Kirschvink 1981.)

quantitatively defined by the Langevin function (Fig. 4; Kirschvink 1981), i.e., the accuracy of the compass response should increase asymptotically with external field strength. The third prediction is that the threshold sensitivity to changes in magnetic field intensity will be defined by the first derivative of the equation for the root mean square deviation of the crystals' alignment in the intensity receptor organelle. Plotted against external field strength the threshold sensitivity should increase to a maximum at about 50 μT (= 0.5 Gauss) and decline monotonically thereafter (Fig. 5; J.L. Kirschvink and M.M. Walker unpublished).

These predictions are testable with currently available behavioral conditioning procedures. The first prediction is testable using the conditioning paradigm reported here. A factorial design is suggested in which experiments test for separate responses to magnetic field direction and intensity. The tests require fish to discriminate between magnetic fields with different vector directions but the same total intensity and between fields with the same direction but different intensities. The second and third predictions are testable with suitable modifications of the conditioning procedure used for testing sun-compass orientation in

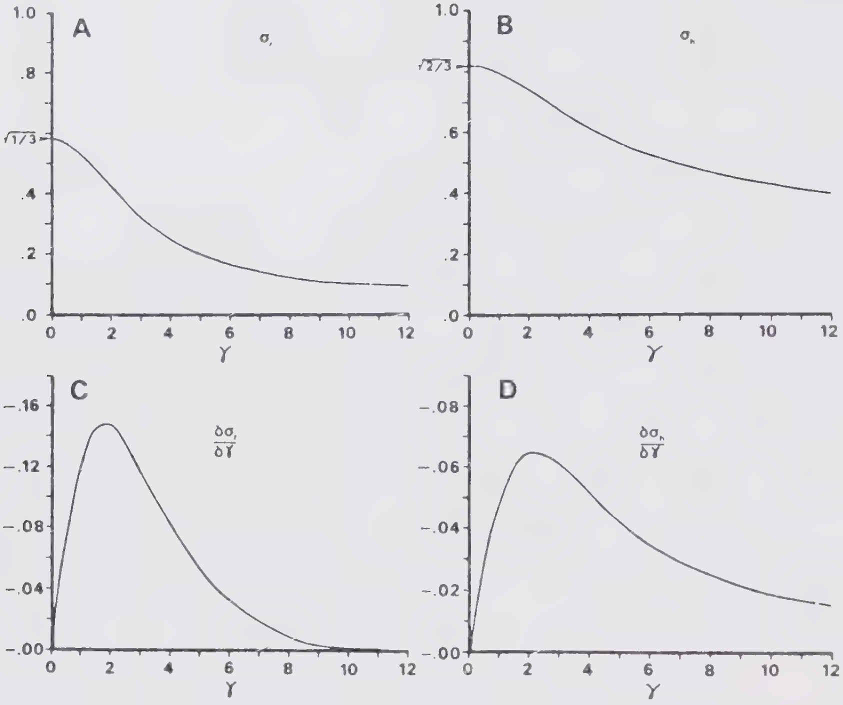

Figure 5. A,B. Plots of the variance of the Langevin function parallel and perpendicular to external field direction against γ, the ratio of magnetic to thermal energies of single domain magnetite crystals. C,D. Plots of the first derivative of the Langevin variance parallel and perpendicular to external field direction. The Langevin variance declines with increasing γ, and, for magnetite-based magnetoreceptors, will be dependent on external field intensity. It follows that receptors monitoring some component of this variance will be most sensitive to changes in intensity when the change in variance with intensity is a maximum. C,D show that the maximum rates of change of variance with intensity occur at about γ = 2. Behaviorally measured thresholds to magnetic field intensity changes should follow the form of these plots. Threshold sensitivity should increase rapidly with external field intensity to a maximum and decline thereafter. (J.L. Kirschvink and M.M. Walker, unpublished data.)

white bass by Hasler et al. (1958). The accuracy of a directional response should increase asymptotically with magnetic field strength and should conform to the Langevin function (Fig. 4) (Kalmijn 1981; Kirschvink 1981). The same conditioning approach can be adapted to test for the smallest changes in magnetic field intensity that the fish can detect. Fish should be required to produce or withhold a single response with accuracies approaching 90-100%. Threshold sensitivity is then measured by decreasing the difference between positively and negatively reinforced stimuli using appropriate procedures Engen 1971). This threshold sensitivity to magnetic field intensity changes should change with field strength in the manner shown in Fig. 5 (J.L. Kirschvink and M.M. Walker unpublished).

CONCLUDING REMARKS

This and other recent studies have demonstrated repeatable behavioral responses to magnetic fields by migratory fishes (Quinn 1980; Quinn et al. 1981; Quinn and Brannon 1982). Theoretical analyses based on the physical properties of single-domain magnetite discovered in yellowfin tuna and other animals easily explain the separate magnetic compass and intensity responses of vertebrates and invertebrates (Yorke 1979, 1981; Kirschvink 1981; Kirschvink and Gould 1981). J.L. Kirschvink and M.M. Walker (unpublished) extend these analyses and make testable predictions on the nature and organization of ferromagnetic magnetoreceptor organelles and the constraints they place on the capacities of the magnetic sense.

Gross dissection of the anterior region of the skull of yellowfin tuna reveals the supraophthalmic nerve. This trunk carries the anterior acousticolateralis nerve and ramifies in the region of the ethmoid bones. The hair cells associated with the acousticolateralis nerve system could provide ideal mechanoreceptors for use in magnetoreception with the magnetite crystals. Preliminary histological studies suggest the presence of nerves in a thin band of tissue in the midline immediately beneath the dermethmoid bone (Walker unpublished data). Thus for the first time there is found together in a species a repeatable behavioral response to magnetic fields and the necessary physical and neural components of a ferromagnetic sense organ. Proving the links between these components of a magnetic sense should be an important goal for future research.

It now seems opportune to speculate on the possible utility of the magnetic sense of pelagic fishes for navigation. Acoustic tracking experiments have shown that swordfish *Xiphias gladius* can maintain a compass heading for periods of up to several days (Carey and Robison 1981). Skipjack tuna make diurnal horizontal movements without retracing their path onto and off shallow banks where they feed during daylight hours (Yuen 1970). These movements suggest that these fishes are able to determine their position and set a compass course toward a goal. The knowledge that pelagic fishes respond to magnetic fields suggests the possibility that they use the geomagnetic field to guide their migrations. Field experiments to test this hypothesis should not only show whether fish do use the geomagnetic field in navigation but may also indicate how the fish use the sense. This should contribute greatly to our understanding of the mechanisms of migration in fishes.

ACKNOWLEDGMENTS

A.E. Dizon, J.T. Corwin, J.L. Kirschvink and staff and graduate students at the National Marine Fisheries Service, Kewalo Research Facility have contributed to this paper through critical discussions and comments on an earlier draft. Research funds from the National Marine Fisheries Service, and travel funds from the University of Hawaii and this Institute are gratefully acknowledged.

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A Candidate Magnetic Sense Organ in the Yellowfin Tuna, *Thunnus albacares*

Abstract. *Single-domain magnetite crystals have been isolated and characterized from tissue located in a sinus within the dermethmoid bone of the skull of the yellowfin tuna,* Thunnus albacares. *Their chemical composition, narrow size distribution, and distinctive crystal morphology indicate that these crystals are biochemical precipitates. Experiments on the interaction between particles reveal the organization of the particles in situ and suggest a possible form for candidate magnetoreceptor organelles. The consistent localization of such particles with similar arrangement within the dermethmoids of this and other pelagic fishes suggests that the ethmoid region is a possible location for a vertebrate magnetic sense organ.*

Magnetic material has been detected in the tissues of various metazoan species (*1–5*). Although the material is inferred to be magnetite, in many cases this has not yet been established, and external contaminants have not been excluded as possible sources of magnetic remanence. Even in the homing pigeon and the honey bee, detailed localization of the magnetite has proved difficult to ascertain, and the particles have not been isolated or characterized previously (*3, 4*). For many of the species studied, behavioral evidence for magnetic sensitivity is lacking or in dispute.

Earlier we reported reproducible conditioned responses to earth-strength magnetic fields in the yellowfin tuna, *Thunnus albacares* (*6*). We now report the detection, extraction, and characterization of magnetite crystals from tissue within a sinus formed by the dermethmoid bone of the skull of this species. The crystals have a narrow size distribution, are single magnetic domains, and have morphologies similar to other biochemically formed magnetites. Studies of the interactions between particles suggest that the crystals are arranged in groups or chains in the dermethmoid tissue. Magnetite-based magnetoreceptor organelles arranged in vivo in a form consistent with these observations could provide these fish with a sensitive magnetoreception system.

To distinguish magnetic material with a possible magnetoreceptive function from other deposits, we sought to identify a tissue with the following characteristics: (i) it should have a high remanent magnetic moment concentrated in a small volume of sample compared with other tissues from the same fish; (ii) the anatomical position of the magnetic tissue must be consistent from fish to fish; (iii) the bulk magnetic properties, including particle coercivity, should be similar in different individuals and in different species of fish; and (iv) it should be innervated.

Tissue and organ samples, including bones of the body and the skull, skin, sense organs, viscera, and swimming muscles, were dissected from three 1-year-old yellowfin tuna (fork length, 40 to 50 cm) with glass microtome knives and handled with nonmetallic tools in a magnetically shielded, dust-free clean room. Although subsequent dissections focused on the most magnetic tissue, other samples were measured in all fish. Samples were washed in glass-distilled water, frozen in liquid nitrogen, exposed to strong fields from a cobalt-samarium magnet or an air-core impulse solenoid (*7*), and tested for isothermal remanent magnetization (IRM) in a superconducting magnetometer. We extracted the magnetic material for other tests by combining the magnetic tissue from several fish, grinding the tissues in a glass tissue grinder, extracting released fats with ether, digesting the remaining cellular material in Millipore filtered 5 percent sodium hypochlorite solution (commercial bleach), and briefly treating the residue with 0.5*M* EDTA (*p*H 7.1). After centrifuging and washing, aggregates of black particles could be separated magnetically from the residue; control samples of originally nonmagnetic tissues yielded no such product. The magnetic

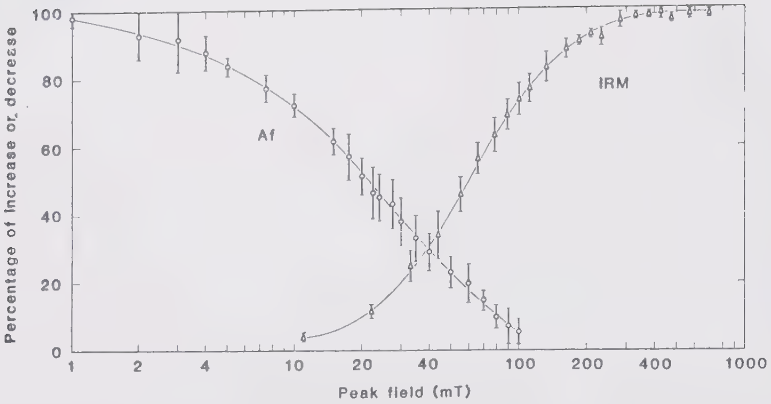

Fig. 1. The one-axis Af demagnetization and IRM acquisition curves for the dermethmoids of four yellowfin tuna. Saturation magnetization (1 to 3 × 10^3 pA·m^2) is 100 percent and natural remanent magnetization is 0 percent in both plots. Error bars represent standard errors of the means.

powder extracted from the dermethmoid tissue was analyzed by x-ray diffraction, electron microprobe, and transmission electron microscopy (TEM).

Of 17 tissues and organ samples examined for magnetic remanence, 15 had mean moments less than 500 pA·m^2, and two (eye tissue and dermethmoid bone) had moments greater than 1000 pA·m^2 (*8*). The intensities of magnetization of these samples identified the frontal and dermethmoid bones as the samples containing the greatest concentrations of magnetic material (*8*). Subdivision and remeasurement of the dermethmoids from a number of fish suggested that the magnetic material was contained in a sinus formed within the dermethmoid bone. Because the dermethmoid bones acquired greater moments (260 to 3000 pA·m^2) than the frontal bones (59 to 300 pA·m^2) and were always clearly magnetic, we focused our remaining studies on the dermethmoid bone and on the tissue it contained in particular.

The frozen dermethmoid tissues of seven yellowfin tuna had natural remanent magnetization moments at or below the instrument noise level (< 50 pA·m^2). We magnetized these samples (600 to 3000 pA·m^2) and allowed them to warm to room temperature, measuring their moments at 5-minute intervals. The moments retained by the samples all decayed with time, although not all lost their moments completely within the period of the experiments (1 hour). This observation suggests that, as the tissues thawed, the orientation of the magnetic particles became randomized through thermal agitation.

We washed and refroze the dermethmoids of four fish, subjected them to magnetic fields of progressively increasing strength with the impulse solenoid, and then demagnetized them with progressively increasing alternating fields (Af). The magnetic moment remaining after each step in these procedures was measured in the magnetometer. The dermethmoids acquired virtually all of their magnetization in fields between 10 and 200 mT and lost it again in alternating fields between 10 and 100 mT (Fig. 1). The absence of the multi-domain magnetite particles detected by Zoeger *et al.* (*5*) in the Pacific dolphin, *Delphinus delphis*, is indicated by the flatness of the Af demagnetization curve below peak fields of 10 mT. The almost complete saturation of the samples in fields above 200 mT rules out the presence of hematite and metallic iron alloys, which will continue to acquire remanence in fields above 1000 mT.

If the magnetic particles producing the moment were uniformly dispersed throughout the dermethmoid tissue, the IRM acquisition and Af demagnetization curves would be symmetrical about the 50 percent magnetization point. This follows because magnetic moments that are aligned by a given impulse field level should also be moved by an alternating field of the same strength. Interactions between the particles aid Af demagnetization and inhibit IRM acquisition, displacing the curves and causing their intersection to fall below the 50 percent magnetization point (*9*). However, the abscissa of the intersection point still provides a good estimate of the median coercivity of magnetic particles in the sample (*9*). The ordinate and the abscissa of the intersection of the Af demagnetization and IRM acquisition curves for the yellowfin tuna dermethmoids were at 30 percent magnetization and 40 mT, respectively (Fig. 1). These data are compatible with the presence of about 8.5 × 10^7 single-domain magnetite particles in the dermethmoid tissue; these particles are approximately 50 nm in length, have axial ratios of about 0.8 (*10*), and are organized into interacting groups or chains (*9, 11*).

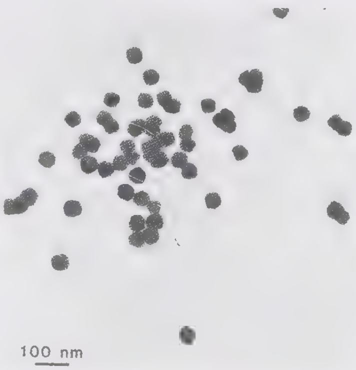

Fig. 2. Isolated magnetite crystals from the yellowfin tuna dermethmoid tissue. Scale bar is 100 nm.

An x-ray diffraction pattern identified magnetic particles extracted from the dermethmoid tissue as crystalline magnetite (*12*). Electron microprobe (Cameca MBX) analysis showed that the crystals were pure, containing no measurable titanium, chromium, or manganese (*11*). In TEM, the isolated crystals were 45 ± 5 nm in length and 38 ± 5 nm in diameter (mean ± standard error of the mean) (Fig. 2). These dimensions fall within the single-domain stability field of magnetite (*13*), and their sizes and axial ratios match the particle coercivities measured in whole tissues. The crystals do not conform to the octahedral crystal morphology or lognormal size-frequency distributions normally shown by geologic or synthetic magnetites (*14*). Nonoctahedral crystal habits and uniform size distributions are characteristic of chiton and bacterial magnetites (*15*), which suggests that crystal morphology is a useful means of distinguishing biologic from nonbiologic magnetites (*15, 16*).

The properties and organization of the magnetite particles in the dermethmoid tissue of the yellowfin tuna meet preconditions for use in magnetoreception and suggest a possible form for magnetite based magnetoreceptors. Their chemical composition, uniform size, and biologically distinctive morphology are evidence of closely controlled biomineralization processes and, consequently, magnetic properties. The crystals will have a coupling energy with the geomagnetic field of about 0.1 kT. They are therefore too small to contribute individually to magnetoreception since their net alignment, as given by the Langevin function, will be poor (*17*). Organization of the particles into chains similar to those in the magnetosomes of magnetotactic bacteria (*18*) will yield greater coupling energies and is consistent with the interactions between the particles detected in the dermethmoid tissue. The decay with warming of the IRM acquired by the dermethmoid tissue indicates that the particle groups are at least partially free to rotate. Taken together, these results suggest an association of the particles with a mechanoreceptor that detects the position or movement of the groups. Theoretical analyses (*19*) show that chains of 20 to 60 particles would provide ideal coupling energies with the geomagnetic field for use in magnetoreception. Assuming that the 8.5×10^7 particles detected in the dermethmoid tissue are arranged in such a fashion, a magnetite-based magnetoreception system in the yellowfin tuna could resolve magnetic field direction to within a few seconds of arc, or magnetic field intensity differences of 1 to 100 nT (*19*).

Gross dissection of the dermethmoid region of the yellowfin tuna revealed the supraophthalmic trunk nerve, which carries branches of the trigeminal, facial, and anterior lateral line nerves and which ramifies in the ethmoid region. Histological studies have suggested the presence of nerve axons in the dermethmoid tissue (*20*). A suitable physical and possible neural basis for previously demonstrated behavioral responses to magnetic fields has thus been demonstrated for the first time in one species. Our magnetometry results are consistent in phylogenetically distant fishes (*12*) and, along with similar results for other vertebrates (*1, 4, 5*), suggest that the ethmoid region of the skull is a likely site for a vertebrate magnetic sense organ.

Note added in proof: Magnetite crystals isolated from the dermethmoid tissue of chinook salmon, *Oncorhynchus tshawytscha*, are organized in chains when viewed in TEM (*21*).

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8. Samples with mean moments less than 500 $pA \cdot m^2$: liver, pyloric caecum, intestine, red muscle, white muscle, brain, parietal bone, gill, skin, peduncle tendon, frontal bone, pectoral fin, posterior brain case, dorsal fin, cardiac muscle. Samples with mean moments greater than 1000 $pA \cdot m^2$: eye (1242 ± 526.3, $N = 4$), dermethmoid bone (1320.6 ± 224.0, $N = 15$). Background signal in the magnetometer was less than or equal to 50 $pA \cdot m^2$. All samples had intensities of magnetization (that is, moments per gram of tissue) less than or equal to 62.5 pT except the frontal bones (44.3, 162.9 pT) and dermethmoid bones (127.0 ± 32.8 pT, $N = 7$).
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Scorpaeniformes: Development

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THE Scorpaeniformes are the fourth largest order of fishes encompassing about 20 families (depending on classification used), 250 genera and over 1,000 species. Representatives of the order are widely distributed from tropical to arctic and antarctic waters. Most scorpaeniforms are benthic or epibenthic with representatives ranging from freshwater to the deep ocean.

The morphologically diverse "mail-cheeked fishes" are named for the bony suborbital stay which extends posteriorly from the third infraorbital to the preopercle. The suborbital stay is the only known character that defines the order; however, some workers have suggested that the stay evolved independently in several lineages and may not indicate monophyly (Matsubara, 1943; Quast, 1965; Poss, 1975). The classification of the scorpaeniforms is controversial, not only in terms of monophyly but also at the subordinal and familial levels. Discussion of the taxonomic status and current hypotheses of relationships is presented in Scorpaeniformes: Relationships (this volume).

Modes of reproduction vary widely within the scorpaeniforms. Many families spawn individual pelagic eggs (Anoplopomatidae, Congiopodidae, Hoplichthyidae and Triglidae), while others spawn demersal clusters of adhesive eggs (Agonidae, Cottidae, Cyclopteridae and Hexagrammidae). Where known, most scorpaenids produce pelagic egg masses enclosed in a gelatinous matrix. Notable exceptions include the scorpaenid genus *Sebastes* and the comephorids of Lake Baikal which give birth to live young.

Larvae of only about 20% of scorpaeniform genera and approximately 10% of the species are known. Because of the wide diversity of form, we are not able to characterize a typical scorpaeniform larva. Early life stages of many scorpaeniforms are characterized by strong head spination as depicted in the generalized scorpaenid larva *Sebastes* (Fig. 220). However, the expression of head spination is variable within the order with elaborations and losses in many groups.

For the purposes of this paper, we consider the Scorpaeniformes to be monophyletic and utilize the broad suborders Scorpaenoidei and Cottoidei as a framework for presentation and discussion. Because of the order's morphological diversity and the lack of an agreed upon classification, discussion of larval taxonomy is focused upon each family. The scorpaeniform family Cyclopteridae is presented in the subsequent article in this volume.

SCORPAENOIDEI

Eggs

Eggs are known for seven of the scorpaenoid families recognized in Washington et al. (this volume), however, they are known only for a few species (Table 107). Most scorpaenoid families are oviparous and spawn pelagic eggs; however, reproductive modes are varied in the Scorpaenidae. In the scorpaenid subfamilies Scorpaeninae, Pteroinae, and Sebastolobinae the eggs are extruded in bilobed gelatinous egg masses which float at the surface. The eggs are slightly elliptical and have homogeneous yolk, a narrow perivitelline space, and a smooth chorion. A single oil globule is present in *Pterois* (0.16–0.17 mm) and *Sebastolobus* (0.18–0.20 mm); *Scorpaena* lacks an oil globule. In the choridactyline genus *Inimicus,* eggs are extruded singly, are spherical, and lack an oil globule (Table 107). Members of the scorpaenid subfamily Sebastinae are viviparous and give birth to large broods of young which are comparable in stage of development to first-feeding larvae of oviparous scorpaenids. The eggs are retained in the lumen of the ovary after ovulation, range between 0.75 and 1.9 mm, have homogeneous yolk, a narrow perivitelline space, smooth chorion, and one to many oil globules. For the other families for which eggs are known, the eggs are pelagic with none to multiple oil globules (Table 107).

Larvae

At least one larval stage is known for 64 of the more than 600 species of scorpaenoids and for 20 of the 100+ genera. Major reviews of larval scorpaenoids include Sparta (1956b)

Table 107. Summary of Eggs and Larval Size Characteristics of the Scorpaeniformes based on Available Literature (excluding Cyclopteridae).

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at			References
					Hatching	Flexion	Transformation	
Scorpaenoidei								
Scorpaenidae								
Sebastinae[1]								
Sebastes capensis	V	—	—	—	3.8	6.2–7.0	ca. 20	Moser et al., 1977
S. fasciatus	V	—	—	—	ca. 5.8	8.5–10.0	—	Moser et al., 1977; Fahay, 1983
S. marinus	V	1.5	—	—	6.7–7.2	8.5–11.8	ca. 24	Moser et al., 1977; Tåning, 1961
S. viviparous	V	—	—	—	5.4–5.8	7.8–10.6	—	Tåning, 1961
S. hubbsi	V	—	—	—	ca. 4.4	ca. 6	—	Uchida et al., 1958
S. inermis	V	—	—	—	4.5	ca. 7	ca. 18	Harada, 1962
S. longispinis	V	1.36	1	—	5.8–6.1	6.4–7.1	—	Takai and Fukunaga, 1971
S. marmoratus	V	0.75–0.95	1	0.2	ca. 4.5	ca. 8	ca. 17	Tsukahara, 1962
S. nigricans	V	1.6	many to 1	—	6.9–7.0	—	ca. 10	Fujita, 1957b, 1959
S. oblongus	V	1.56–1.60	many	—	7.2–7.5	ca. 8.5	12–14	Fujita, 1958
S. pachycephalus	V	1.5–1.9	many	—	6.0–7.0	ca. 8	>13	Shiokawa and Tsukahara, 1961
S. schlegeli	V	—	—	—	ca. 6.1	—	—	Sasaki, 1974
S. steindachneri	V	—	—	—	ca. 4.8	—	—	Sasaki, 1974
S. taczanowskii	V	—	—	—	ca. 5.4	—	—	Sasaki, 1974
S. constellatus	V	—	—	—	4.0–5.0	<7.1	—	Moser and Butler, in press
S. cortezi	V	—	—	—	4.1	7.0–8.3	ca. 17	Moser et al., 1977
S. crameri	V	—	—	—	ca. 5.7	8.0–9.3	16–21	Westrheim, 1975; Richardson and Laroche, 1979
S. dallii	V	—	—	—	5.0	6.2–8.0	<20	Moser and Butler, 1981
S. entomelas	V	—	—	—	4.5–4.6	9.9–12.9	21.7–30.6	Laroche and Richardson, 1981; Moser and Butler, in press
S. flavidus	V	—	—	—	4.5	—	23.6–26.7	DeLacy et al., 1964; Laroche and Richardson, 1980
S. helvomaculatus	V	—	—	—	4.1	7.7–8.0	12.0–18.6	Richardson and Laroche, 1979; Westrheim, 1975
S. jordani	V	—	—	—	5.4	8.0–10.0	27–30	Moser et al., 1977
S. levis	V	—	—	—	5.0	7.6–10.4	ca. 19	Moser et al., 1977
S. macdonaldi	V	—	—	—	4.0–5.0	7.7–9.0	ca. 15	Moser et al., 1977
S. melanops	V	—	—	—	—	—	23.2–30.6	Laroche and Richardson, 1980
S. melanostomus	V	—	—	—	4.5	6.2–7.2	ca. 16	Moser and Ahlstrom, 1978
S. ovalis	V	—	—	—	4.9–5.1	ca. 6.8	—	Moser and Butler, in press
S. paucispinis	V	1.0	1	ca. 0.20	4.6	7.2–9.7	15	Moser et al., 1977
S. pinniger	V	—	—	—	4.0	ca. 7.8	12.8–18.4	Waldron, 1968; Richardson and Laroche, 1979
S. rufus	V	—	—	—	4.6–4.8	6.1–7.6	—	Moser and Butler, in press
S. zacentrus	V	—	—	—	ca. 4.3	7.4–8.5	13.7–19.6	Laroche and Richardson, 1981; Westrheim, 1975
Sebastes Type A	V	—	—	—	4.2	7.0–7.6	—	Moser et al., 1977
Helicolenis dactylopterus	V	—	—	—	2.2	6.0–7.9	>19	Graham, 1939; Sparta, 1956b; Tåning, 1961; Moser et al., 1977; Fahay, 1983
Scorpaeninae								
Pontinus Type A	—	—	—	—	<2.3	4.1–4.6	ca. 15	Moser et al., 1977
Pontinus Type B	—	—	—	—	—	<5.0–5.5	ca. 10	Moser et al., 1977

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at			References
					Hatching	Flexion	Transformation	
Scorpaena guttata	P	1.22–1.29 × 1.16–1.19	0	—	1.9–2.0	4.5–5.7	>13	David, 1939; Orton, 1955d; Moser et al., 1977
S. notata	P	0.76 × 0.88	0	—	<2.7	ca. 6.0	—	Sparta, 1956b
S. porcus	P	0.84 × 0.92	0	—	1.72	ca. 6.7	ca. 12	Sparta, 1956b
S. scrofa	P	0.68 × 0.88	0	—	<2.8	ca. 6.0	ca. 17	Sparta, 1956b
Scorpaena Type A	—	—	—	—	ca. 2.0	4.0–5.5	>12	Moser et al., 1977
Scorpaenodes xyris	—	—	—	—	1.8	4.0–5.4	11–14	Moser et al., 1977
Pteroinae								
Pterois lunulata	P	0.81–0.83	1	0.16–0.17	1.52–1.58	—	—	Mito and Uchida, 1958; Mito, 1963
Dendrochirus brachypterus	P	—	0	—	ca. 1.1	—	—	Fishelson, 1975
Sebastolobinae								
Sebastolobus alascanus	P	1.2–1.4	1	0.18–0.20	ca. 2.6	6.0–7.3	14–20	Pearcy, 1962; Moser, 1974; Moser et al., 1977
S. altivelis	P	1.2–1.4	1	0.18–0.20	ca. 2.6	6.0–7.3	14–20	Moser et al., 1977
Setarchinae								
Ectreposebastes imus	—	—	—	—	<2.8	ca. 5.5	ca. 28	Moser et al., 1977
Choridactylinae								
Inimicus japonicus	P	1.31–1.43	0	—	3.18–3.27	6.4–8.2	ca. 10.4	Fujita and Nakahara, 1955; Mito, 1963; Sha et al., 1981
Minoinae								
Minous sp. (?)	—	—	—	—	ca. 1.8	3.7–5.9	>9.0	Leis and Rennis, 1983
Triglidae								
Chelidonichthys cuculus	P	1.45–1.65	1	—	—	—	—	Padoa, 1956e
C. gurnardus	P	1.45–1.5	1	0.19–0.33	3.2	9.0	17.0	Padoa, 1956e
C. kumu	P	1.20–1.27	1	0.25–0.27	3.12–3.26	—	—	Uchida et al., 1958
C. lastoviza	P	1.29–1.33	1	0.24	—	—	—	Padoa, 1956e
C. lucerna	P	1.25–1.36	1	0.26–0.28	3.2	9.0	17.0	Padoa, 1956e
C. obscurus	P	—	—	—	—	—	—	Padoa, 1956e
Lepidotrigla alata	P	1.22–1.25	1	0.25	2.78–2.92	—	—	Mito, 1963
L. aspera	P	1.16	1	0.21–0.22	3.2	7.0	19.0	Padoa, 1956e
L. japonica	P	1.20–1.40	1	0.25–0.26	—	—	—	Mito, 1963
L. microptera	P	1.26–1.31	1	0.25–0.28	—	—	—	Mito, 1963
Prionotus carolinus	P	0.94–1.15	10–25	—	2.6–2.8	—	8.6	Fritzsche, 1978; Fahay, 1983
P. evolans	P	—	—	—	—	6.3	8.7	Fahay, 1983
Peristediidae								
Peristedion	P	1.7	—	—	—	<11.5	15.0	Padoa, 1956e; Breder and Rosen, 1966
Congiopodidae								
Congiopodus leucopaecilus[2]	P	1.9–2.2	0	NA	—	—	—	Robertson, 1974, 1975a
C. spinifer[2]	P	1.82	0	NA	5–6	—	>12.4	Brownell, 1979; Gilchrist, 1904; Gilchrist and Hunter, 1919; Robertson, 1975a
C. torvus[2]	P?	1.7–1.8	0	NA	—	—	—	Gilchrist, 1904
Platycephalidae								
Platycephalus indicus[2]	P	0.88–1.2	1	0.19–0.25	1.78–2.3	7.3	13	Ueno and Fujita, 1958; Chang et al., 1980
Platycephalidae spp.	—	—	—	—	~2.1	3.9–5.2	—	Leis and Rennis, 1983

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at Hatching	Body length (mm) at Flexion	Body length (mm) at Transformation	References
Hoplichthyidae								
Hoplichthys haswelli[2]	P	0.85–0.90	1	0.15	—	—	—	Robertson, 1975a
Hoplichthys sp.[2]	—	—	—	—	—	≳8	—	Okiyama (unpubl. MS)
Dactylopteridae								
Dactylopterus volitans	P	~0.8	1	0.14	1.8	<7	ca. 16	Fritzsche, 1978; Sanzo, 1933c; Padoa, 1956e
Daicocus petersoni	—	—	—	—	—	4.3	ca. 10	Senta, 1958
Dactyloptena sp.	—	—	—	—	—	3.9–6.5	ca. 10	Leis and Rennis, 1983
COTTOIDEI								
Agonidae								
Agonomalus mozinoi	D	~1.0	—	—	5.5	—	—	Marliave, 1978
Agonopsis chiloensis[2]	—	—	—	—	—	—	—	de Ciechomski, 1981
Agonus cataphractus	D	1.7–2.2	Several co-alesce	0.7–0.75	6.3–8.0	—	~14 mm	Russell, 1976; Ehrenbaum, 1904; McIntosh and Prince, 1890
A. decagonus[2]	—	—	—	—	—	—	—	Ehrenbaum, 1905–1909
Aspidophoroides monopterigius[2]	—	—	—	—	—	—	—	Dannevig, 1919; Bigelow and Schroeder, 1953
A. olriki[2]	—	—	—	—	—	—	—	Dunbar, 1947
Bothragonus swani	D	2	—	—	7.5	~10–12	>16	Marliave, 1975
Pallasina barbata[2]	—	—	—	—	—	—	—	Marliave, 1975
Xeneretmus latifrons[2]	—	—	—	—	~7	~10	—	Marliave, 1975
Anoplopomatidae								
Anoplopoma fimbria	P	2.0–2.1	—	—	<8.8	11–14	>33	Ahlstrom and Stevens, 1976; Hart, 1973; Kobayashi, 1957
Comephoridae								
Comephorus baicalensis	V	N/A	—	—	9.4	—	>48	Chernyayev, 1975
C. dybowskii	V	N/A	—	—	8.2	~13	~21	Chernyayev, 1971
Cottidae								
Artedius creaseri	—	—	—	—	~3.5	5.7–7.9	13–14	Washington, 1981
A. fenestralis	—	—	—	—	3.5–3.8	5.9–6.8	12–13	Washington, 1981; Marliave, 1975
A. harringtoni	—	—	—	—	~3.0	5.2–6.4	12–14	Washington, 1981
A. lateralis	D	1.07	1	0.22	3.9–4.5	5.0–6.3	9.5–10.5	Washington, 1981; Marliave, 1975; Budd, 1940
A. meanyi	—	—	—	—	~3	6.3–9.4	15–20	Washington, 1981
Ascelichthys rhodorus	D	1.7–2.0	—	—	6.0	8.8–9.0	12–15	Matarese and Marliave, 1982
Blepsias cirrhosus[2]	—	—	—	—	—	≲11	—	Marliave, 1975; Richardson, 1981a
Chitonotus pugetensis[2]	D	1.02–1.05	1 large 5–8 small	0.3	2.9–3.0	—	>16	Misitano, 1980; Richardson and Washington, 1980
Clinocottus acuticeps	D	1.0–1.2	—	—	3.1–3.3	5.5–7.3	12.6–15.0	Washington, 1981; Washington, pers. obs.
C. analis[2]	D	1.2–1.3	several large	0.18	4.2–4.5	—	—	Budd, 1940; Washington, 1981
C. embryum	—	—	—	—	~4.0	6.4–9.6	13–14	Washington. 1981
C. globiceps	D	1.5–2.0	—	—	5.1–5.4	6.2–8.1	12.9–13.5	Washington, 1981
C. recalvus	D	1.25–1.35	—	—	4.6–4.7	—	9–11	Morris, 1951
Cottus asper	D	—	—	—	5.5–6.3	~7.0	—	Stein, 1972; Richardson and Washington, 1980
C. bairdi	D	1–3	1	—	6.3–6.9	—	9–10	Heufelder, 1982
C. carolinae	D	2.6–3.3	—	—	6.80	—	9.5–10	Wallus and Granneman, 1979
C. cognatus	D	2–3	—	—	5.7–6.3	—	8–11	Wallus and Granneman, 1979
C. nozawae	D	3.1–3.5	—	—	10.5	—	—	Watanabe, 1976
C. reinii[2]	D	2.0–2.6	1	—	—	—	—	Watanabe, 1976

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at			References
					Hatching	Flexion	Transformation	
C. ricei[2]	D	—	—	—	7–8	—	—	Heufelder, 1982
Enophrys bison	D	1.7–1.8	1	0.36	4.9–5.2	5.2–7.0	7.6–7.8	Misitano, 1978; Richardson and Washington, 1980
E. bubalis (*Taurulus*)	D	1.5–1.8	several	—	5.5–5.8	—	12	Russell, 1976
E. lilljeborgi (*Taurulus*)[2]	D	2.0	1	0.38	~4.0	—	—	Russell, 1976
Gymnocanthus herzensteini	D	1.6–1.7	few	—	5.6–6.1	—	—	Kyushin, 1970
G. ventralis[2]	—	—	—	—	—	—	—	Ehrenbaum, 1905–1909
Hemilepidotus gilberti[2]	—	—	—	—	—	—	—	Hattori, 1964
H. hemilepidous	D	1.5–1.6	1	0.31–0.56	~5–6	~9.1	>19–23	Richardson and Washington, 1980
H. jordani	—	—	—	—	—	—	—	Gorbunova, 1964a[6]
H. spinosus	—	—	—	—	~5	7.6–10.1	19	Richardson and Washington, 1980
H. zapus	—	—	—	—	—	7–12	—	Matarese and Vinter (in prep.)
Hemitripterus americanus	D	4	1 large	0.8	10–14	~14.5	>18.8	Fahay, 1983; Fuiman, 1976
H. villosus	D	—	—	—	10.9–11.6	≲14.4	~20	Okiyama and Sando, 1976
Icelus bicornis[2]	—	—	—	—	—	—	—	Russell, 1976; Ehrenbaum, 1905–1909
Leptocottus armatus[2]	D	1.4–1.5	present	—	3.9–4.8	~8	15–20	Richardson and Washington, 1980; Jones, 1962
Myoxocephalus aenaeus	D	1.5–1.7	2+	0.2	4.7–6.3	6.8	—	Fahay, 1983; Lund and Marcy, 1975
M. octodecimspinosus	D	1.9–2.3	1 or more	diameter varies	6.3–7.3	9–11	~15	Fahay, 1983; Colton and Marak, 1969
M. quadricornus	D	1.5–2.2[3]	—	—	~8	ca. 10.5+	—	Khan and Faber, 1974
M. scorpius	D	1.8–2.5	several	0.4–0.5	7.4–8.6	9–15	17–20	Russell, 1976; Ehrenbaum, 1905–1909; McIntosh and Masterman, 1897
M. thompsoni[2]	—	—	—	—	8–10	—	—	Heufelder, 1982
Nautichthys oculofasciatus	D	2–2.5	—	—	9	~9–11	~26	Richardson and Washington, 1980; Marliave, 1975
Oligocottus maculosus	D	1.3–1.5	1 large many small	—	4.2–4.5	7.2–7.6	7.5–10	Washington, 1981; Stein, 1973
O. snyderi	D	1.2–1.3	—	—	4.47	6.2–8.4	11–13	Washington, 1981; Stein, 1972
Orthonopias triacis[2]	D	0.9–1.0	1 large 2 small	—	2.9–3.8	—	—	Bolin, 1941
Paricelinus hopliticus[2]	—	—	—	—	<5.6	—	~25	Richardson and Washington, 1980
Pseudoblennius cottoides[2]	D	2.0–2.2	—	—	12.5	—	—	Watanabe, 1976
Radulinus asprellus	—	—	—	—	≲4.7	7.2–10.9	≳15	Richardson and Washington, 1980
R. boleoides[2]	—	—	—	—	—	~8.7	—	Richardson and Washington, 1980
Rhamphocottus richardsoni	D	2.5–2.8	—	—	6–7	8.4	~14–15	Richardson and Washington, 1980; Marliave, 1975; Blackburn, 1973
Scorpaenichthys marmoratus	D	1.4–1.9	1 large several small	0.27	5.8–6.0	7.5–8.7	14–15[4]	Richardson and Washington, 1980; O'Connell, 1953
Triglops murrayi[2]	—	—	—	—	7–8	12	—	Fahay, 1983
T. pingeli[2]	D	2.0	many	—	—	—	—	Bigelow and Schroeder, 1953; Rass, 1949
Cottocomephoridae								
Abyssocottus bergianus[2]	D	3.2–3.3[3]	—	—	—	—	—	Taliev, 1955
A. godlewskii[2]	D	2.8–3.0[3]	—	—	~5	—	—	Taliev, 1955
A. korotneffi[2]	D	~4.5[3]	—	—	—	—	—	Taliev, 1955

TABLE 107. CONTINUED.

Family/subfamily species	Type of egg pelagic (P), demersal (D) or viviparous (V)	Egg size (mm)	Number of oil globules	Largest oil globule size (mm)	Body length (mm) at			References
					Hatching	Flexion	Transformation	
A. pallidus[2]	D	2.6–2.8[3]	—	—	~6	—	~16	Taliev, 1955
Asprocottus gibbosus[2]	D	3.3–3.4[3]	—	—	—	—	—	Taliev, 1955
A. herzensteinii[2]	D	3.0–3.2[3]	—	—	—	—	≳9	Taliev, 1955
A. megalops[2]	D	3.5–3.7[3]	—	—	—	—	—	Taliev, 1955
Batrachocottus baicalensis	D	~3.0	3–10 small	—	10.0 post-flexion[5]	N/A	~16	Chernyayev, 1981
B. multiradiatus[2]		~4.0	—	—	~6.0	—	—	Taliev, 1955
B. nikolskii[2]	D	2.9–3.1	—	—	—	—	—	Taliev, 1955
B. uschkani[2]	—	—	—	—	—	—	—	Taliev, 1955
Cottinella boulengeri[2]	D	2.8[3]	—	—	—	—	—	Taliev, 1955
Cottocomephorus grewingki	D	1.2–1.8	—	—	~6.8–7.0	—	~19	Taliev, 1955
C. inermis[2]	D	1.5–1.7	—	—	—	—	—	Taliev, 1955
Paracottus kessleri	D	1.0–1.45	1 large	0.3	5.2–5.4	~6.2	~20	Chernyayev, 1978
P. kneri	D	2.0–2.3	—	—	6.8–7.1	—	>10.8	Taliev, 1955
Procottus jeittelesi[2]	D	2.5–3.3	—	—	—	—	—	Taliev, 1955
Hexagrammidae								
Hexagrammos agrammys	D	2.02–2.07	many coalesce to 1	—	8.15–8.61	~11	≲40–48	Fukuhara, 1971
H. decagrammus	D	—	—	—	ca. 8	15–18	~30[4]	Kendall and Vinter, 1984
H. lagocephalus	D	2.0–2.6	many	—	~8–9	12–15	ca. 29	Kendall and Vinter, 1984; Gorbunova, 1964b (as *H. decagrammas*)
H. octogrammus	D	1.75–2.10	many	0.8	6–7	~12–15	~30[4]	Gorbunova, 1964b
H. otakii	D	2.3–2.7	many	—	6.5–7.0	~11	—	Gorbunova, 1964b; Yusa, 1960c
H. stelleri	D	—	—	—	~7–9	~12–15	~30[4]	Kendall and Vinter, 1984
Ophiodon elongatus	D	2.9–3.2	1	—	~9.0	11–15	~30[4]	Kendall and Vinter, 1984
Pleurogrammus monopterygius	D	2.1–2.8	many	1.38–1.4	10–11	~14–19	~30[4]	Yusa, 1967; Gorbunova, 1964b
Oxylebius pictus	D	—	—	—	4–5	7–9	~45	Kendall and Vinter, 1984; DeMartini, 1976
Zaniolepis sp.	—	—	—	—	~2.5	~6	?15	Kendall and Vinter, 1984
Normanichthyidae								
Normanichthys crockeri	—	—	—	—	<4.4	7–9	>16	Balbontin and Perez, 1980
Psychrolutidae								
Dasycottus setiger[2]	—	—	—	—	—	~10	—	Richardson, 1981a
Gilbertidia sigalutes[2]	D	2.3	—	—	—	~13–15	~23	Marliave, 1975
Malacocottus sp.	—	—	—	—	—	~7–9.8	≲24	Richardson, 1981a
Psychrolutes paradoxus[2]	—	—	—	—	—	~10.5	~13–14	Marliave, 1975

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[1] Ovarian or newborn larvae of 30 species of *Sebastes* not listed here are described in Efremenko and Lisovenko (1970), Westrheim (1975), and Moser et al. (1977).

[2] Incomplete description with illustration.

[3] Ripe ovarian egg diameter.

[4] Pelagic juvenile stage.

[5] Hatch at advanced postflexion stage.

[6] Confusion exists regarding correct identification [Matarese and Vinter (in prep.)].

and Moser et al. (1977) on scorpaenids and Sparta (1956b) and Richards (in prep.) on triglids and peristediids.

Scorpaenidae (Figs. 220–223).—This is the largest and most diverse scorpaenoid family with about 44 genera and more than 350 species. The classification and relationships of the family are in controversy (Washington et al., this volume) and we follow their subfamily groupings.

Sebastinae.—Barsukov (1981) includes 3 genera and 114 species in this temperate and boreal group. *Sebastes* with about 106 species accounts for almost ⅓ of the species in the order. At least a single larval stage is known for 62 species of *Sebastes* and flexion or postflexion stages have been described for about 32 of these (Table 107). Larval stages have been described for one of the 6 species of *Helicolenus* and are unknown for the two species of *Hozukius*.

In *Sebastes* most of the yolk is utilized before hatching while the eggs lie freely within the ovary. Hatching precedes extrusion and newborn larvae range from 3.8 to 7.5 mm in length among the various species and have functional eyes, jaws, and pectoral fins. The finfold is slightly inflated and has minute cell-like

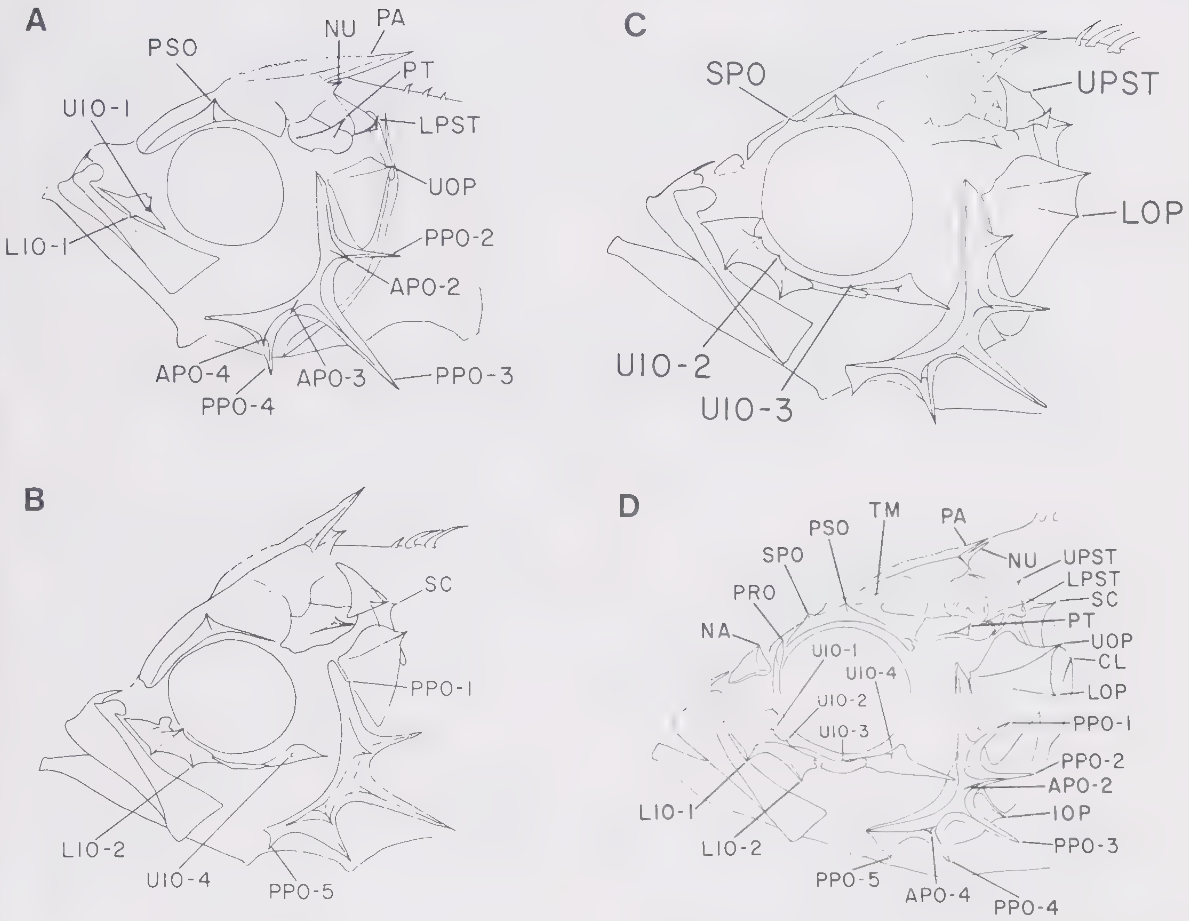

Fig. 220. Head spines in 6.2 mm (A), 8.2 mm (B), 10.0 mm (C) and 16.0 mm (D) stained larvae of *Sebastes melanostomus*. Abbreviations of head spines: APO-2, 2nd anterior preopercular; APO-3, 3rd anterior preopercular; APO-4, 4th anterior preopercular; CL, cleithral; IOP, interopercular; LIO-1, 1st lower infraorbital; LIO-2, 2nd lower infraorbital; LOP, lower opercular; LPST, lower posttemporal; NA, nasal; NU, nuchal; PA, parietal; PPO-1, 1st posterior preopercular; PPO-2, 2nd posterior preopercular; PPO-3, 3rd posterior preopercular; PPO-4, 4th posterior preopercular; PPO-5, 5th posterior preopercular; PRO, preocular; PSO, postocular; PT, pterotic; SC, supracleithral; SPO, supraocular; TM, tympanic; UIO-1, 1st upper infraorbital; UIO-2, 2nd upper infraorbital; UIO-3, 3rd upper infraorbital; UIO-4, 4th upper infraorbital; UOP, upper opercular; UPST, upper posttemporal. From Moser and Ahlstrom, 1978.

structures concentrated along the dorsal and ventral margins. Notochord flexion occurs at about 6–12 mm and transformation at 15–25 mm (Table 107). Many species have a distinct pelagic juvenile stage which can reach almost 60 mm body length.

Preflexion larvae have a slender body (body depth 13–23% of body length) and compact gut; snout–anus distance increases from about 40–50% of body length to over 60% in some species during the larval period. The caudal and pectoral fins begin forming first, followed by the pelvics and then the dorsal and anal fins. The pectoral fins range from short and rounded to elongate and fan-shaped, reaching almost 50% of body length in *S. levis* (Fig. 221). The pectoral fin base is shallow (typically 7–13% of body length) in comparison with other subfamilies. Ossification of skeletal elements begins early in the larval period and proceeds rapidly as in other scorpaenoids; vertebral ossification follows the pattern of other scorpaeniforms, with the neural arches ossifying before the centra (Moser, 1972).

Pigmentation in newborn larvae consists of a melanistic sheath over the gut and a postanal series along the ventral midline. Some species also have a dorsal midline series which may develop gradually. Pigment increases with development, appearing on the head (above brain, on jaws and opercular region), fins, and caudal peduncle. Often the pectoral fins (both base and blade) have diagnostic pigment patterns. Several of the western Pacific species are heavily pigmented with the head and body covered by a sheath of melanophores (Fig. 221).

Head spines are a prominent feature of all *Sebastes* larvae. Pterotics, parietals (usually serrated), and preopercular spines

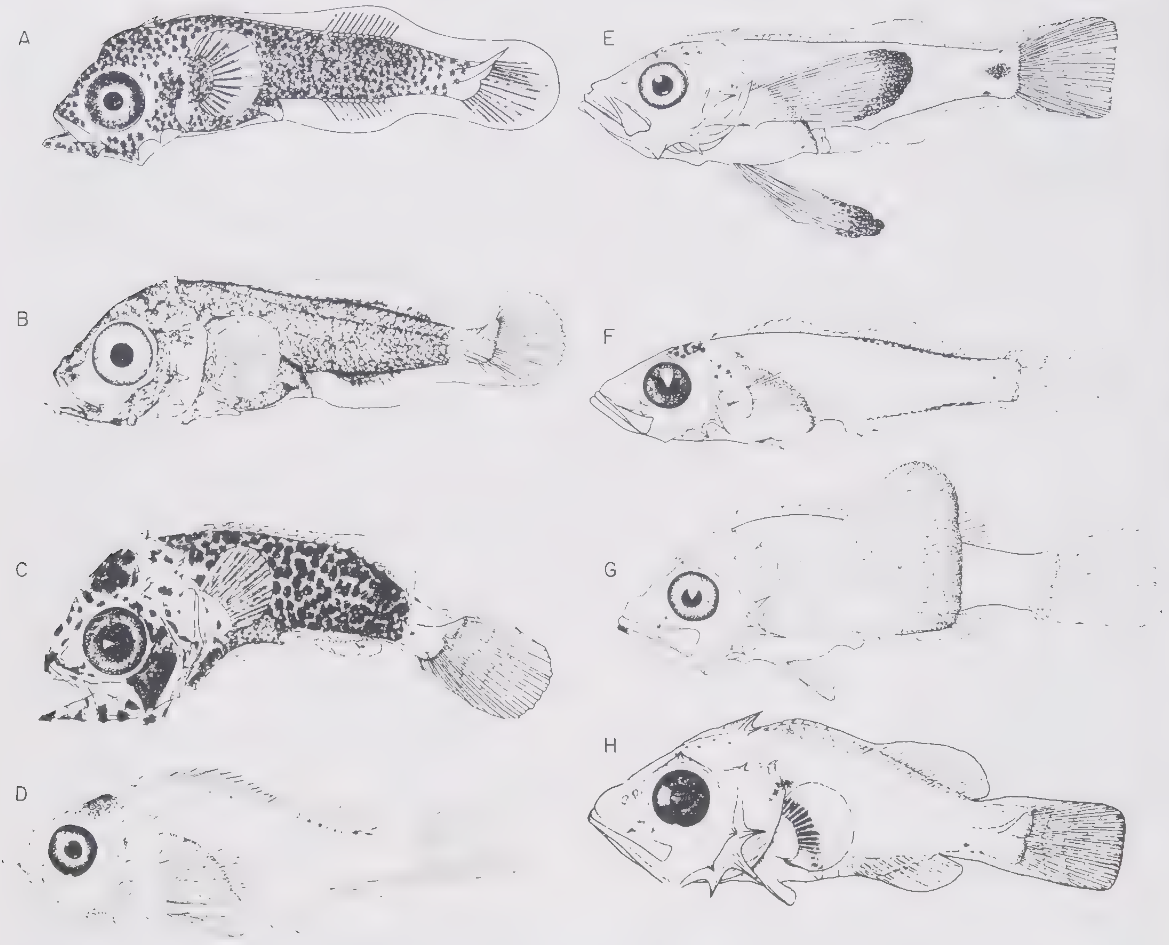

Fig. 221. Larvae of Scorpaenidae. (A) *Sebastes oblongus,* 8.5 mm TL (from Fujita, 1958); (B) *S. longispinis,* 7.1 mm TL (from Takai and Fukunaga, 1971); (C) *S. hubbsi,* 6.0 mm TL (from Uchida et al., 1958); (D) *S. zacentrus,* 12.7 mm SL (from Laroche and Richardson, 1981); (E) *S. paucispinis,* 10.5 mm SL (from Moser et al., 1977); (F) *S. jordani,* 15.5 mm SL (ibid.); (G) *S. levis,* 10.4 mm SL (ibid.); (H) *Helicolenus dactylopterus,* 10.0 mm (from Tåning, 1961).

form during the preflexion period in most species, and other spines appear gradually thereafter (Fig. 220). Although there is variation in larval spine complements (Moser and Ahlstrom, 1978; Moser and Butler, 1981; Richardson and Laroche, 1979; Laroche and Richardson, 1980, 1981), it is apparent that 1) the adult head spine complement develops during the larval period and 2) certain spines develop during the larval period but are not present in adults. Of the latter, the most prominent are the pterotic, anterior preoperculars, lower posttemporal, and upper infraorbitals.[1] The fact that these spines do occur in adults of other subfamilies is of possible phylogenetic significance (Moser and Ahlstrom, 1978).

Helicolenus is viviparous, the fertilized eggs developing in a gelatinous matrix within the ovary (Graham, 1939; Krefft, 1961). Larvae of *H. dactylopterus* have been described; hatching and birth occur at a smaller size (2.2 mm) than in *Sebastes,* although sizes at notochord flexion and transformation are similar (Table 107). Larvae are moderately deep-bodied (Fig. 221); body depth averages 29%, 33%, and 49% of body length for preflexion, flexion and postflexion stages. Head and gut shape are similar to that of *Sebastes.* The pectoral fin is moderate in size and rounded; the base is slightly deeper than in most species of *Sebastes.* Sequence of fin formation is similar to that of *Sebastes.* A mass of spongy tissue develops anteriorly in the dorsal finfold in preflexion larvae and persists through most of the larval period; the structure is apparently unique. The early pigment pattern consists of a dorsolateral gut sheath, melanophores above the brain, on the lower jaw, in a short median ventral series just

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[1] Upper infraorbitals are present in adults of a few species of *Sebastes.*

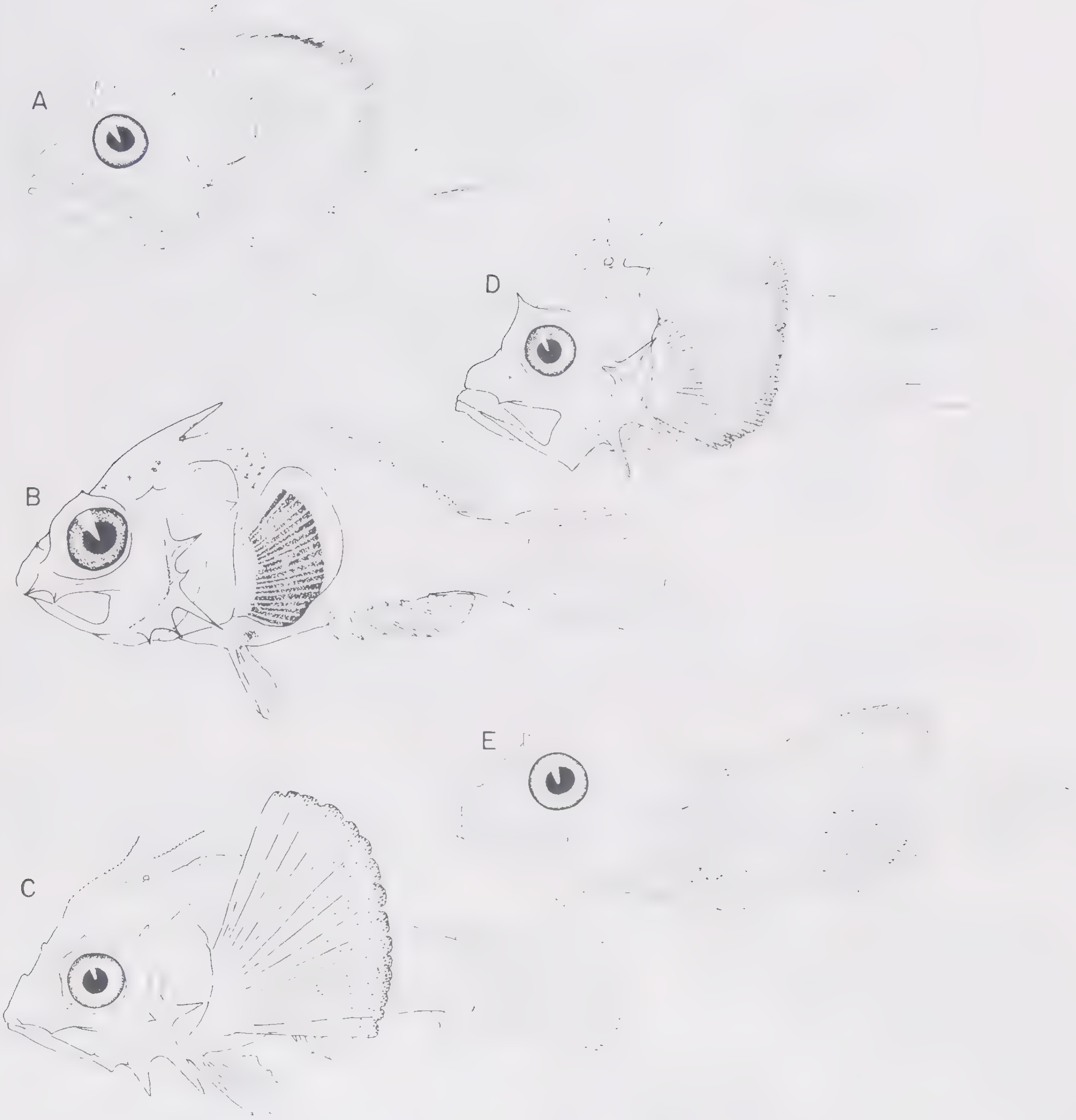

Fig. 222. Larvae of Scorpaenidae. (A) *Pontinus* Type A, 8.0 mm SL (from Moser et al., 1977); (B) *Scorpaena* Type A, 8.0 mm SL (ibid.); (C) *Scorpaenodes xyris*, 6.2 mm SL (ibid.); (D) *Sebastolobus* sp. 7.7 mm SL (ibid.); (E) *Ectreprosebastes imus*, 6.7 mm SL (ibid.).

anterior to the caudal fin, and on the distal and proximal regions of the pectoral fin blade (Fig. 221). Head spine formation is similar to that of *Sebastes* species which have full larval complements, except that spines are lacking on the 2nd infraorbital bone and the cleithrum.

Scorpaeninae.—Larval stages are known for only 3 of the 15 genera in this subfamily; a total of 8 species (or generic types) out of about 150 have been described (Table 107; see Sparta, 1956b and Moser et al., 1977, for major reviews). Hatching occurs at about 2.0 mm or less; newly-hatched larvae have a large elliptical yolk sac, unpigmented eyes, pectoral fin buds, and lack a mouth. The finfold is inflated and, along with the body skin, forms a balloon-like envelope that is attached principally at the snout and pectoral regions (Orton, 1955d). Cell-like granulations cover the entire envelope but are concentrated

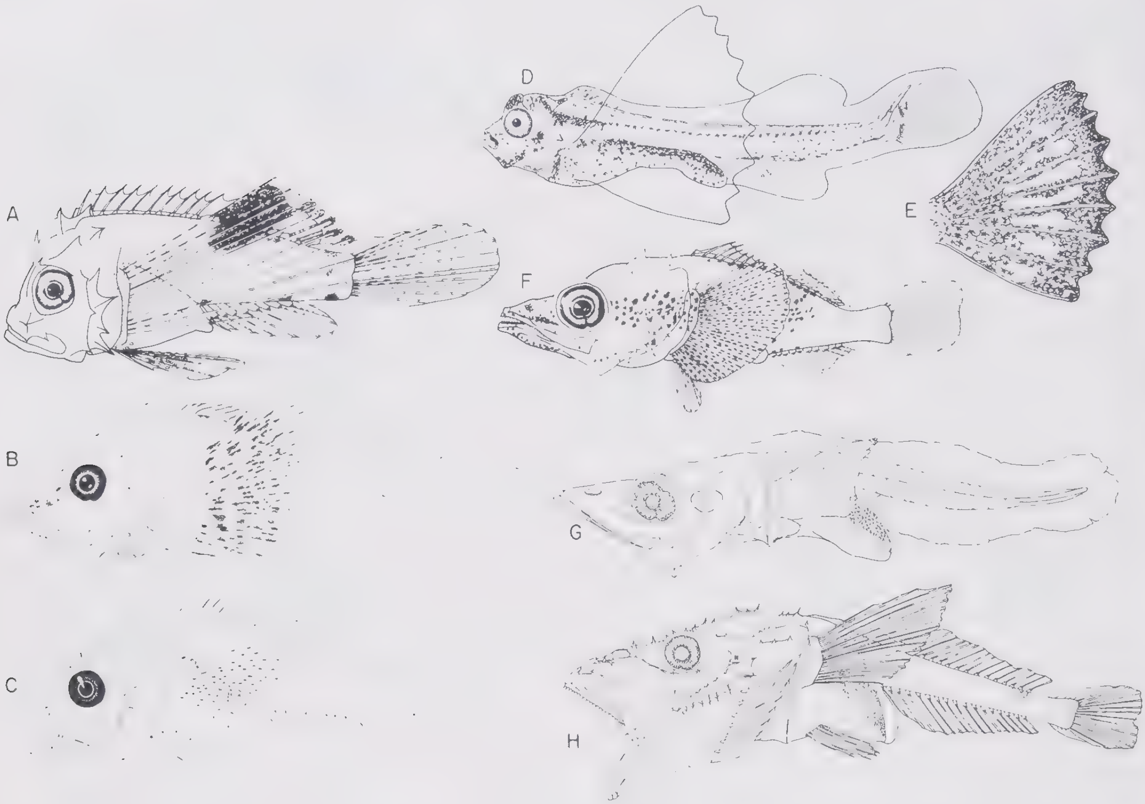

Fig. 223. Larvae of Minoinae (A), Triglidae (B, C), Congiopodidae (D, E), Platycephalidae (F), Hoplichthyidae (G, H). (A) *Minous* sp.?, 6.4 mm SL (from Leis and Rennis, 1983); (B) *Prionotus* sp., 6.4 mm SL (original); (C) *Prionotus stephanophrys*, 8.8 mm SL (CalCOFI 7510 sta. 117.70); (D) *Congiopodus spinifer*, 10.8 mm SL (from Brownell, 1979); (E) Detail of pectoral fin of *Congiopodus spinifer* (ibid.); (F) Platycephalidae, unidentified, 6.2 mm SL (from Leis and Rennis, 1983); (G) *Hoplichthys* sp., 7.1 mm SL (original, courtesy M. Okiyama); (H) *Hoplichthys* sp. 17.2 mm SL (ibid.).

at the median edges of the finfold. Flexion occurs at a small size (4–6 mm) as does transformation (10–17 mm). Larvae are relatively deep-bodied during preflexion and flexion and more so during postflexion, when body depth averages 38–40% of body length for the genera listed in Table 107. The gut is compact and the head becomes massive. Snout–anus length increases from 46–50% of body length in preflexion larvae to 61–67% in postflexion larvae. The snout has a steep profile (Fig. 222).

The pectoral fins are well developed and deep-based; fin base depth is 13–15% of body length in preflexion larvae and 14–18% in flexion and postflexion larvae. They are fan-shaped and enlarged in *Scorpaenodes*; fin length attains 41% of body length during the postflexion stage. They are smaller but distinctively shaped in *Scorpaena* (fan-shaped with scalloped margin) and *Pontinus* (slightly wing-shaped). Ossification of fin rays, as well as skeletal elements, occurs in early larvae (4–5 mm). The caudal, pectoral, and pelvic rays begin ossifying almost simultaneously, followed immediately by the dorsal and anal fins.

Preflexion larvae have a postanal ventral midline series of melanophores ranging in number from 2–7 in *Scorpaena guttata* to 12–18 in *Scorpaenodes xyris*. The most prominent pigment is on the pectoral fins; typical patterns are a concentration at the distal margin (*Scorpaenodes*, some *Pontinus*, some *Scorpaena* spp.), a solid covering over most of the fin (some *Scorpaena* spp.), or a diagonal bar (some *Pontinus* spp.). A melanistic sheath develops over the dorsal surface of the gut and gas bladder in most species of *Scorpaena*, whereas in *Scorpaenodes* and *Pontinus* only the gas bladder is pigmented Other pigment in *Scorpaena* forms at the cleithral juncture and above the brain (Fig. 222).

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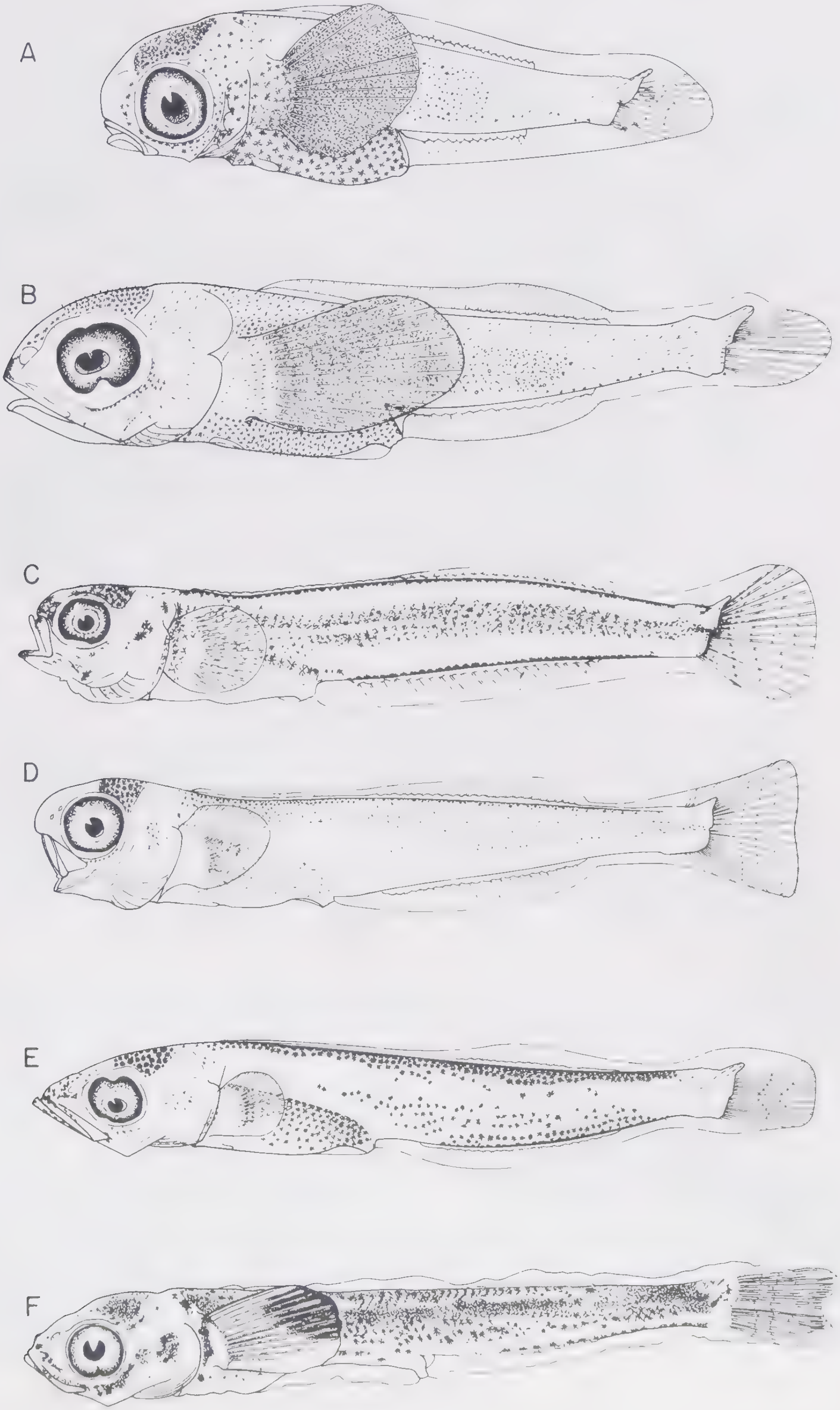
Fig. 224. Larvae of the *Oxylebius* scorpaeniform group (A, B) and the hexagrammid group (C–F) of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Oxylebius pictus*, 8.5 mm SL (from Kendall and Vinter, 1984); (B) *Zaniolepis* sp., 7.7 mm SL (ibid.); (C) *Hexagrammos octogrammus*, 15.2 mm SL (ibid.); (D) *Pleurogrammus monopterygius*, 20.5 mm SL (ibid.); (E) *Ophiodon elongatus*, 15.4 mm SL (ibid.); (F) *Anoplopoma fimbria*, 13.8 mm SL (Ahlstrom and Stevens, 1976).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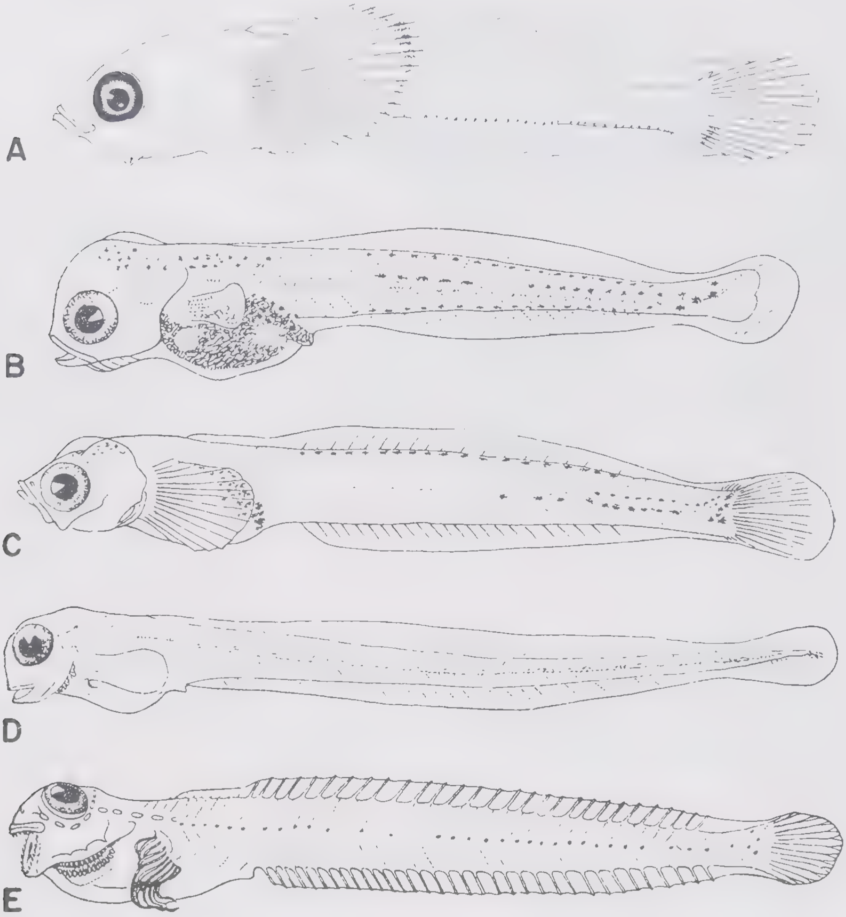


Fig. 225. Larvae of Normanichthyidae (A), Cottocomephoridae (B, C), Comephoridae (D, E). (A) *Normanichthys crockeri,* 8.5 mm SL (original); (B) *Cottocomephorus grewingki,* 7.4 mm (from Taliev, 1955); (C) *Cottocomephorus inermis,* 11.2 mm (ibid.); (D) *Comephorus baicalensis,* 6.9 mm (ibid.); (E) *Comephorus baicalensis,* 21.3 mm (ibid.).

Cranial spine development is similar to that in sebastines. The pterotic, parietal, postocular (supraocular crest), posterior preoperculars (2nd, 3rd, and 4th) anterior preoperculars (2nd and 4th) and lower posttemporal develop during the preflexion period. The lower infraorbital (1st), upper infraorbitals (1st and 4th), posterior preoperculars (1st and 5th), nuchal, supracleithral, cleithral, upper opercular, and lower opercular spines appear during postflexion. Late in the postflexion stage the lower infraorbital (2nd), nasal, preocular, and supraocular spines appear. Spines which do not develop in scorpaenine larvae but are present in adults of most genera are the upper infraorbitals (2nd and 3rd), upper posttemporal, tympanic, and sphenotic. In *Scorpaenodes* the nuchal spine develops during the preflexion period and exceeds the parietal spine in length, giving the parietal ridge a bifurcate appearance. In other scorpaenines and all other scorpaenids except *Sebastolobus,* the nuchal develops late and is excluded from the parietal ridge.

Pteroinae.—Early preflexion larvae have been described for *Pterois lunulata* and *Dendrochirus brachypterus* (Table 107). Newly-hatched larvae are small (1.1–1.6 mm) and similar in morphology to those of Scorpaeninae. The pectoral fins are large and fan-shaped with pigment at the distal margin. Postanal pigment in *Pterois* consists of ventral and dorsal midline series. In *Dendrochirus* this pigment coalesces to form a band.

Sebastolobinae.—Life history series have been described for *Sebastolobus alascanus* and *S. altivelis* (Moser, 1974). Larvae are 2.6 mm at hatching, 6.0–7.3 mm at notochord flexion, and 14–20 mm at transformation. The distinctive pelagic juveniles (up to 56 mm in *S. altivelis*) have a prolonged midwater existence before settling to the deep shelf and slope habitat of the adults. Larval morphology is similar to that of scorpaenines. The pectoral fins are large, deep-based, and fan-shaped (Fig. 222); their rays are the first to ossify, followed by the caudal rays and then

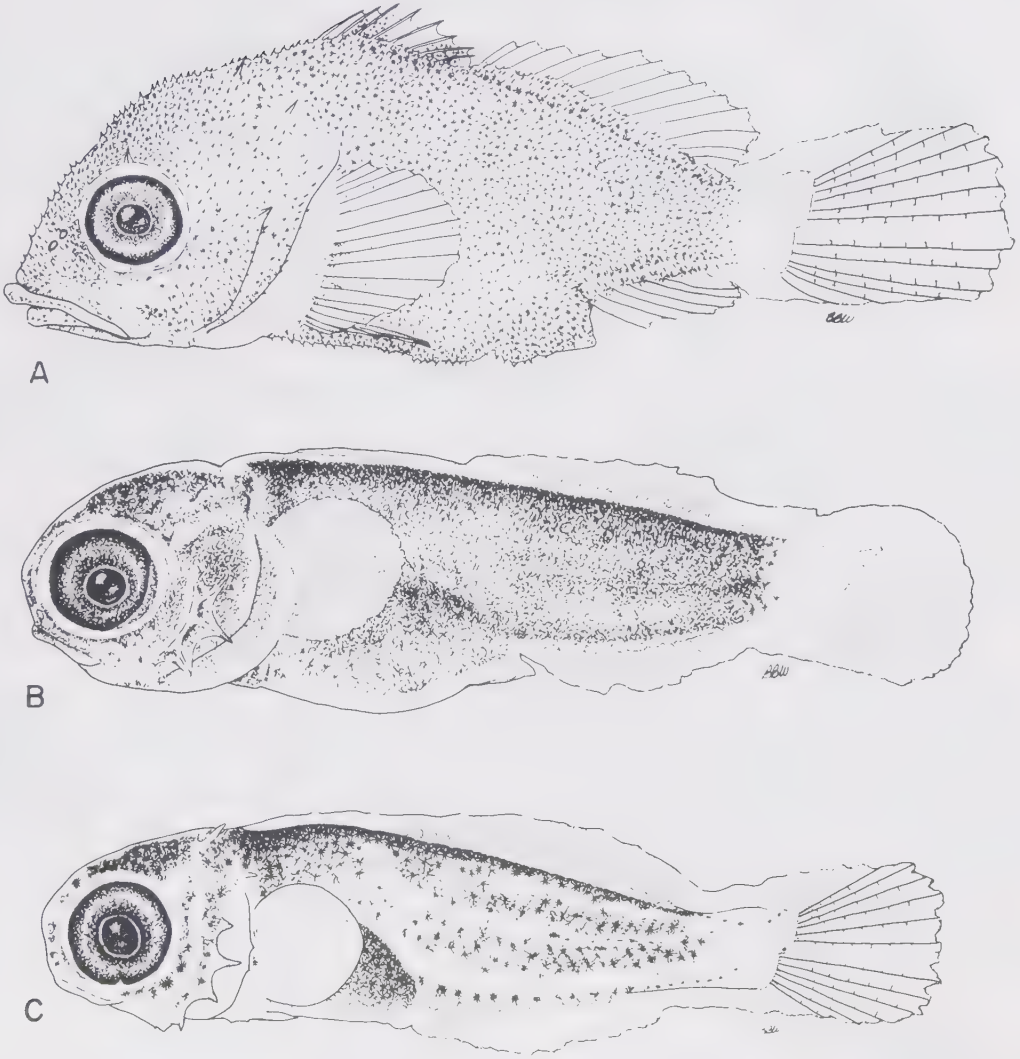
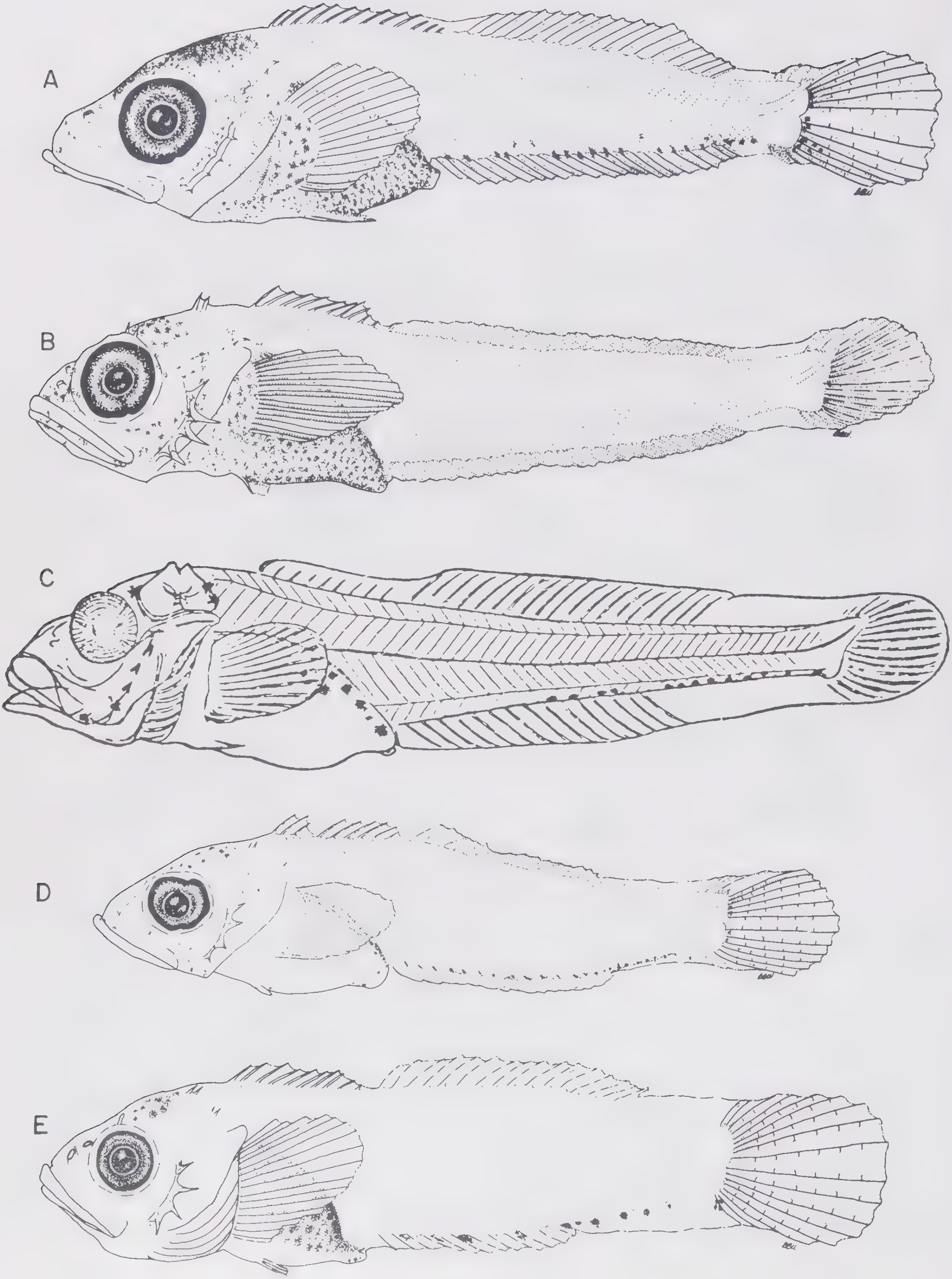


Fig. 226. Larvae of the *Rhamphocottus* group (A) and the *Scorpaenichthys* group (B, C) of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Rhamphocottus richardsoni*, 10.6 mm SL (from Richardson and Washington, 1980); (B) *Scorpaenichthys marmoratus*, 8.7 mm SL (ibid.); (C) *Hemilepidotus spinosus*, 11.0 mm SL (ibid.).

those of the other fins. The pectoral fins are pigmented at the distal margin; other pigment includes a sheath over the gut and melanophores above the brain. Head spination is highly developed (Fig. 222); the sequence of development is similar to that of scorpaenines. In addition to the spine complement of scorpaenines, *Sebastolobus* larvae develop the 2nd and 3rd upper infraorbital spines and the 1st anterior preopercular spine.

Setarchinae.—Larvae are known for *Ectreposebastes imus* (Moser et al., 1977). Hatching and notochord flexion occur at a small size as in the scorpaenines; however, postflexion larvae attain a large size (Table 107). Larvae have the deepest body of known scorpaenids; body depth reaches 55% of body length in late postflexion stage. The gut is compact with an elongate terminal section; snout–anus distance averages 53% of body length in preflexion larvae and 76% in postflexion. The pectoral fins are deep-based, fan-shaped, and large, extending to the caudal peduncle (Fig. 222). Fin base depth and fin length reach 22% and 57% of the body length respectively. The pigment pattern consists of a postanal ventral series of 11–14 melanophores (not present after 4.0 mm), a blotch above the gas bladder, and an almost solid sheath over the pectoral fin, which recedes distally with development. Head spine development is similar to that of scorpaenines.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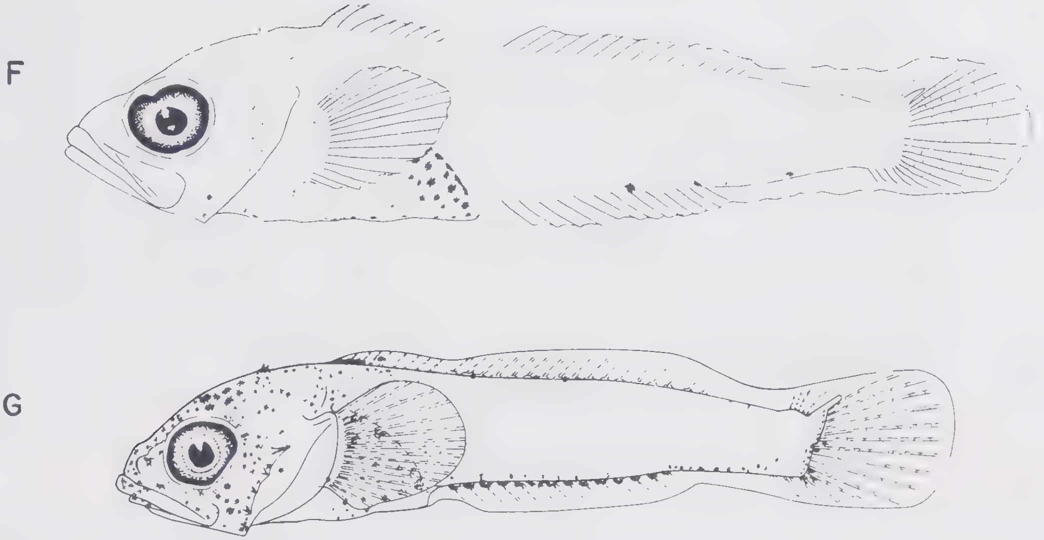


Fig. 227. Larvae of the *Myoxocephalus* group of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Paricelinus hopliticus*, 13.8 mm SL (from Richardson and Washington, 1980); (B) *Triglops* sp., 15.4 mm SL (ibid.); (C) *Icelus bicornis*, 25 mm (from Ehrenbaum, 1905–1909); (D) *Chitonotus pugetensis*, 11.5 mm SL (from Richardson and Washington, 1980); (E) *Artedius meanyi*, 13.8 mm SL (ibid., as *Icelinus* sp.); (F) *Icelinus* sp., 11.9 mm SL (original); (G) *Ascelichthys rhodorus*, 11.0 mm SL (from Matarese and Marliave, 1982).

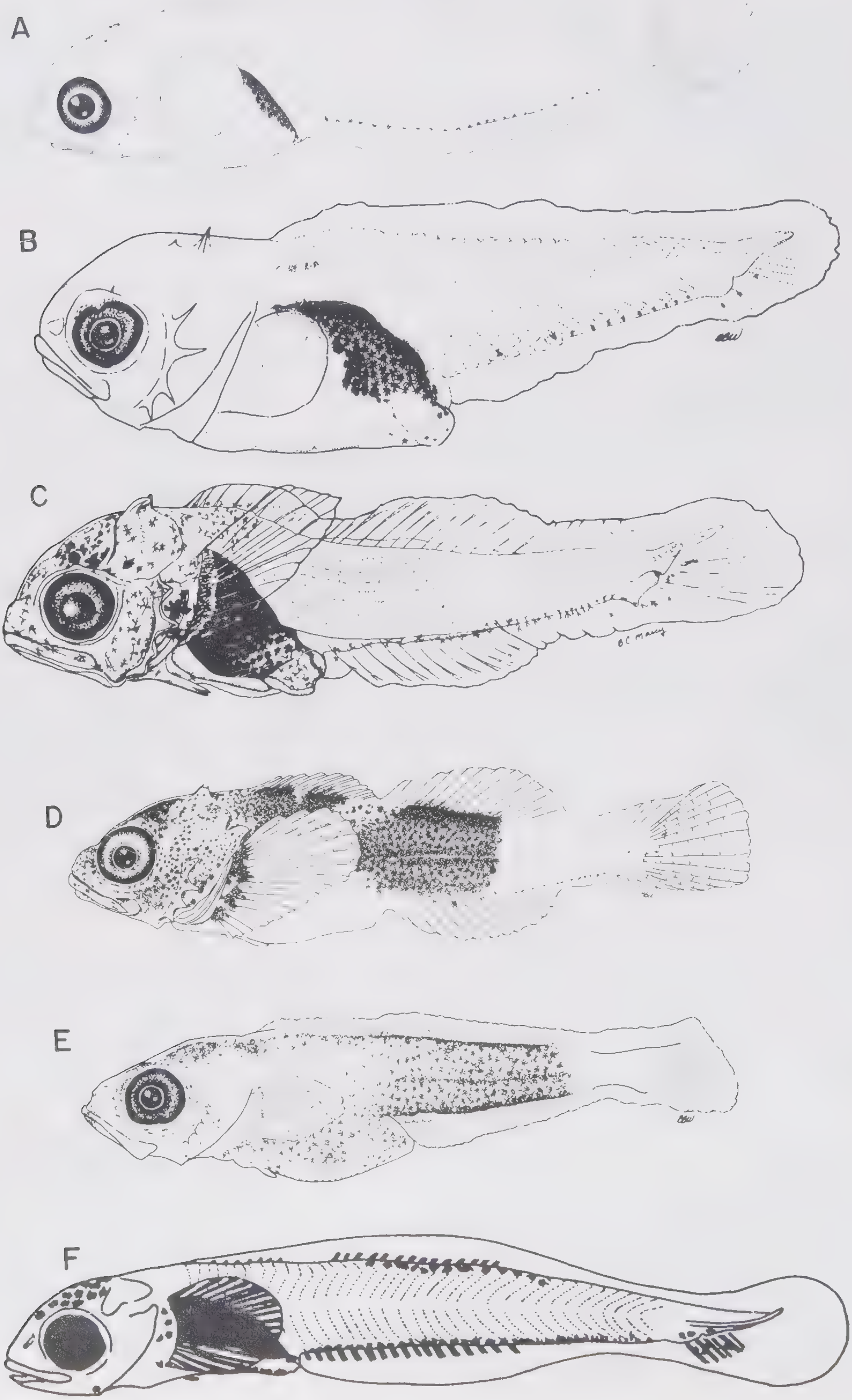
Choridactylinae.—The developmental stages of *Inimicus japonicus* have been described by Fujita and Nakahara (1955) and Sha et al. (1981). Larvae are 3.2 mm at hatching, 6.4–8.2 mm at flexion and about 10 mm at transformation. Yolk-sac larvae are similar to those of Scorpaeninae. Larvae are relatively slender and blunt-headed, with a compact short gut (Fig. 223). The pectoral fins are large and fan-shaped, with a scalloped margin; they develop a series of large blotches distally. One to several large postanal melanistic blotches form on the postanal ventral midline and the gas bladder region is pigmented. Sha et al. (1981) show the larvae to be heavily xanthic.

Minoinae.—Leis and Rennis (1983) described a larval series tentatively identified as *Minous* sp. It is generally similar in morphology and pigmentation to *Inimicus*; however, the pectoral fin is relatively larger and has a different pigment pattern.

Triglidae (Fig. 223).—Eggs are only known for 3 of the 8 genera of triglids. The new world genus *Prionotus* has multiple oil globules whereas single oil globules are known for *Chelidonichthys* and *Lepidotrigla*. Larvae are poorly known with complete series having been described for 4 species in 3 genera (Table 107). There are approximately 90 species in this family and many are very difficult to identify as adults. The genus *Lepidotrigla* has 40+ species and is poorly known in many areas. Diagnostic features include the depressed profile of the head and large pectoral fins of which the lowest three rays become detached during transformation. Meristics are very similar to platycephalids and caution is advised. However, most triglids have fewer pectoral rays than most scorpaenoids. *Prionotus*, including *Bellator*, has 13 to 15 plus 3 free rays; *Trigla, Chelidonichthys, Lepidotrigla*, and *Uradia* have 11 plus 3 free rays; and *Pterygotrigla* and *Parapterygotrigla* have 11 to 13 plus 3.

Peristediidae.—ELH information has been published only for *Peristedion cataphractum* of the eastern Atlantic (Table 107). Larvae and transforming juveniles have elongated upper pectoral rays and strong head spination (see plate 40 in Padoa, 1956e). This family is often combined with the Triglidae, but differs in many characters such as the presence of barbels, 2 rather than 3 free pectoral rays, and the body is encased in bony scutes rather than scales. Three genera (*Heminodus, Paraheminodus* and *Gargariscus*) have jaw teeth and two genera (*Peristedion* and *Satyrichthys*) lack jaw teeth. There are about 25 species found in the tropics of all oceans in deep water (>200 m).

Congiopodidae (Fig. 223).—Eggs are known for only 1 (*Congiopodus*) of the 4 genera of Congiopodidae (Brownell, 1978; Gilchrist, 1904; Robertson, 1974). The pelagic eggs are relatively large (1.7–2.18 mm) and spherical, with a narrow perivitelline space and no oil globules. The egg surface is covered with striations. Early life history stages have been illustrated for one species, *Congiopodus spinifer* (Brownell, 1979; Gilchrist and Hunter, 1919). Robertson (1975a), illustrated a well-developed embryo of *C. leucopaecilus*. Larvae hatch at about 5 to 6 mm NL and are elongate with long guts reaching 50% SL. The pectoral fins are extremely large and fan-shaped. Melanistic pigment is present on the head, nape and on the dorsal and ventral surface of the gut. Two large blotches of pigment on the dorsal and ventral midlines form a band midway between the vent and tail tip. The large pectoral fins have a distal band of pigment which gradually expands over the entire fin with development. Larvae develop large postocular and parietal spines. The presence of preopercular spines can not be determined from the description by Brownell (1975).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Platycephalidae (Fig. 223).—Platycephalids spawn small spherical eggs (<1 mm) with a single oil globule (Chang et al., 1980; Uchida et al., 1958). Larvae have been described and illustrated for *Platycephalus indicus* (Ueno and Fujita, 1958) and for a series of larvae incorporating seven unidentified species (Leis and Rennis, 1983). Newly-hatched platycephalids are relatively small (1.7–2.3 mm) and slender-bodied, with unformed mouths, unpigmented eyes, and large yolk sacs. By the time of yolk absorption larvae have large heads and deep bodies which taper toward the tail. The gut is quite long reaching ⅔ SL during development. The pointed snout becomes distinctively long and flattened. Pigmentation is usually present on the head, jaws, ventral surface of the gut and along the postanal ventral midline. Pigment may also be present on the dorsolateral surface of the tail and pectoral fin. Larvae develop 4 to 9 preopercular spines. Other head spines include: supraocular, supracleithral, parietal and pterotic. Unlike most other scorpaeniforms, head spines persist and become more pronounced in juveniles. Fin development proceeds as follows: pectoral, caudal, dorsal, anal and pelvic.

Hoplichthyidae (Fig. 223).—The pelagic eggs of *Hoplichthys haswelli* are described by Robertson (1975a) as small and spherical with a smooth surface. A single oil globule is present. Descriptions of hoplichthyid larvae have not been published; however, based on Okiyama (in prep.) larvae are quite similar to platycephalids. Preflexion larvae (3.2 mm) are elongate with large heads and pointed snouts. The gut is moderately long (>50% SL) and the early-developing pectoral fins are large and fan-shaped. The snout becomes increasingly long and depressed during development. Pigmentation is limited to the gut, distal tip of the pectoral fin and a band on the ventral finfold midway between the vent and notochord tip. Numerous clusters of small spines develop in the supraocular, parietal and pterotic regions. Seven spines form on the posterior margin of the preopercle with smaller spines at their base. As in platycephalids, head spines persist in juveniles.

Dactylopteridae (Fig. 233).—The pelagic eggs are small (0.8 mm) and slightly ovoid with a single oil globule. The egg surface is smooth and unsculptured. Larvae hatch at about 1.8 mm and undergo flexion of the notochord between 3.9–6.5 mm. Transformation to the juvenile form occurs at about 9 mm. Larvae are moderately deep-bodied with a distinctively blunt snout and small mouth. The gut is long, reaching about 75% SL in postflexion larvae. Pigmentation occurs over the head, gut, along the postanal ventral midline and around notochord tip. Pigmentation increases dramatically over most of the body in postflexion larvae. The distinctive head armature is quite different from all known scorpaeniform larvae and is present in larvae as small as 2.3 mm NL. A small supraoccipital spine is present only during the larval period. The extremely long posttemporal and preopercular spine extend posteriorly to the middle of the anal fin in larvae by about 6.5 mm and persist in juveniles and adults.

COTTOIDEI

Eggs

Eggs are known from representatives of six of the nine cottoid families recognized here (Table 107). Where known, most cottoids spawn demersal, adhesive eggs which often form clusters found under rocks. Eggs are frequently brightly colored, e.g., red, blue, green, yellow. The eggs of *Anoplopoma fimbria* are pelagic. The Comephoridae of Lake Baikal are reported to be viviparous.

Most eggs are spherical and average 1–2 mm in diameter, although eggs as large as 4 mm have been reported in the cottid *Hemitripterus* and some of the cottocomephorids. A single large oil globule, frequently accompanied by several small ones, occurs in many species. The surface of the eggs is often covered by a tough adhesive membrane, and may be smooth as in *Anoplopoma* and *Myoxocephalus aenaeus* (Fahay, 1983) or covered by tiny, radiating canals as in *Artedius lateralis* and *Clinocottus analis* (Budd, 1940).

Larvae

At least one larval stage is known for 88 of the 329+ species and for 46 of the 104 genera of cottoids. Major overviews of larval cottoid taxonomy include: Richardson and Washington (1980) on cottids; Kendall and Vinter (1984) on hexagrammids; Taliev (1955) and Chernyayev (1971, 1975, 1978, 1981) on comephorids and cottocomephorids; and, forthcoming Laroche (in prep.) on agonids.

Larval cottoids exhibit a broad diversity of form. Size at hatching varies from 2 to 12 mm. Planktonic life may be quite brief, several weeks in many cottids, or may be extended up to a year with a special pelagic juvenile stage as in the hexagrammids.

Cottoid larvae exhibit such a diversity of form and development that it is impossible to characterize a generalized "cottoid" larva.

Hexagrammidae (Fig. 224).—Larvae are known for 10 of the 11 species of the hexagrammid genera *Hexagrammos, Pleurogrammus,* and *Ophiodon.* Major works presenting descriptions and illustrations include Kendall and Vinter (1984) and Gorbunova (1964b). Hexagrammids hatch at a relatively large size (6–11 mm NL). Development is gradual from hatching to the juvenile stage with a prolonged epipelagic prejuvenile period (~30–50 mm SL). Larvae have elongate, slender bodies with large eyes. Larval *Hexagrammos* and *Pleurogrammus* have blunt heads, while *Ophiodon* larvae have pointed snouts and large terminal mouths.

Larvae are heavily pigmented especially dorsally. Melanophores are scattered over the head, gut and usually on the dorsal and ventral midlines. The extent of postanal, ventral midline and lateral pigmentation is useful in specific identification.

Fin formation proceeds in the following sequence: caudal, pectoral, second dorsal and anal, first dorsal and pelvic. Larvae exhibit delayed ossification. Vertebral ossification in hexagram-

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Fig. 228. Larvae of the *Myoxocephalus* cottid group of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Orthonopias triacis,* 7.0 mm SL (original); (B) *Enophrys bison,* 7.0 mm SL (from Richardson and Washington, 1980); (C) *Myoxocephalus aenaeus,* 7.0 mm SL (from Lund and Marcy, 1975); (D) *Myoxocephalus polyacanthocephalus,* 12.0 mm SL (from Richardson, 1981a); (E) *Radulinus asprellus,* 10.9 mm SL (from Richardson and Washington, 1980); (F) *Gymnocanthus tricuspis,* 13.0 mm (from Khan, 1972).

mids (and *Anoplopoma*) is similar to that in Scorpaenoidei with the neural and hemal arches ossifying before the associated vertebral centra. Vertebral counts are notably high (47–63). Head spines are absent in larval *Hexagrammos* and *Pleurogrammus* and extremely reduced in *Ophiodon,* with late-stage larvae developing 4 tiny preopercular spines.

Anoplopomatidae (Fig. 224, Table 107).—Larvae of only *Anoplopoma* have been described and illustrated by Kobayashi (1957) and Ahlstrom and Stevens (1976). Early development of *Anoplopoma* is similar to that of the hexagrammids. Larvae hatch at a large size (~9 mm NL) and development is gradual without great changes in form.

Larvae are slender and elongate with pointed snouts and long guts. The distinctive pectoral fins with heavy distal pigmentation are exceptionally large reaching nearly 33% SL late in the larval period. Larvae are heavily pigmented with melanophores over most of the head, gut and lateral surface of the body.

As in hexagrammid larvae, ossification is delayed with the neural and hemal arches ossifying before the associated vertebral centra. Vertebral counts (61–66) are distinctively high. Pectoral fin development is precocious. Head and preopercular spines are absent.

Oxylebius-Zaniolepis (Fig. 224).—*Oxylebius* and *Zaniolepis* are sometimes included in the Hexagrammidae, but are herein treated separately because of the distinctiveness of their larvae from hexagrammids (Washington and Richardson, MS; Kendall and Vinter, 1984). Larvae of *Oxylebius pictus* and *Zaniolepis* sp. are illustrated and described by Kendall and Vinter (1984). Larvae hatch at a small size (2.5–5 mm NL), undergo notochord flexion between 6 and 9 mm NL, and transform to a benthic juvenile at about 15 mm SL.

Oxylebius and *Zaniolepis* are relatively short and deep-bodied with large, bulging guts and rounded snouts. Pectoral fins develop early and are distinctively large and fan-shaped. Pigmentation is heavy over the anterior half of the body in preflexion larvae and increases over the postanal lateral body with development. *Zaniolepis* possesses characteristic snout pigment which is absent in *Oxylebius.* The pectoral fins of both species are densely pigmented.

Head spination is well-developed with preopercular (5 spines in *Oxylebius*; 6–7 in *Zaniolepis*), posttemporal and supracleithral spines present. *Zaniolepis* larvae develop distinctive prickle-scales over most of the body by about 7 mm.

Normanichthyidae (Fig. 225).—Larvae of the monotypic *Normanichthys crockeri* are illustrated and described by Balbontin and Perez (1980). Hatching occurs at a small size (4.4 mm NL) and flexion of the notochord occurs at 7 to 9 mm. Development from hatching to the juvenile stage is gradual without great change.

Larvae are elongate and slender with short, coiled guts and distinctive large pectoral fins. Pigmentation is restricted to the pectoral fins and the ventral midline extending from the isthmus to the tail. In small larvae several large melanophores are present on the dorsal midline.

Distinctive features of larval development include: the absence of head and preopercular spines, delayed ossification, early development of the pectoral fin, and presence of only 5 branchiostegal rays.

Comephoridae (Fig. 225).—The endemic comephorids of Lake Baikal in Russia are reported to be viviparous (Chernyayev, 1971, 1975) and are born at a relatively large size (8.2–9.4 mm) but are not well developed. Flexion of the notochord occurs at about 8.2 to 13 mm. Larvae develop very slowly with transformation occurring 3 or 4 months after birth.

Larvae are extremely slender and elongate with small heads and very short coiled guts. Comephorids are quite different from other cottoids morphologically and are blennioid in appearance. Pigmentation is usually limited to the gut and sometimes in a series along the postanal lateral midline. Four small preopercular spines develop in late-stage larvae; other head spines are absent.

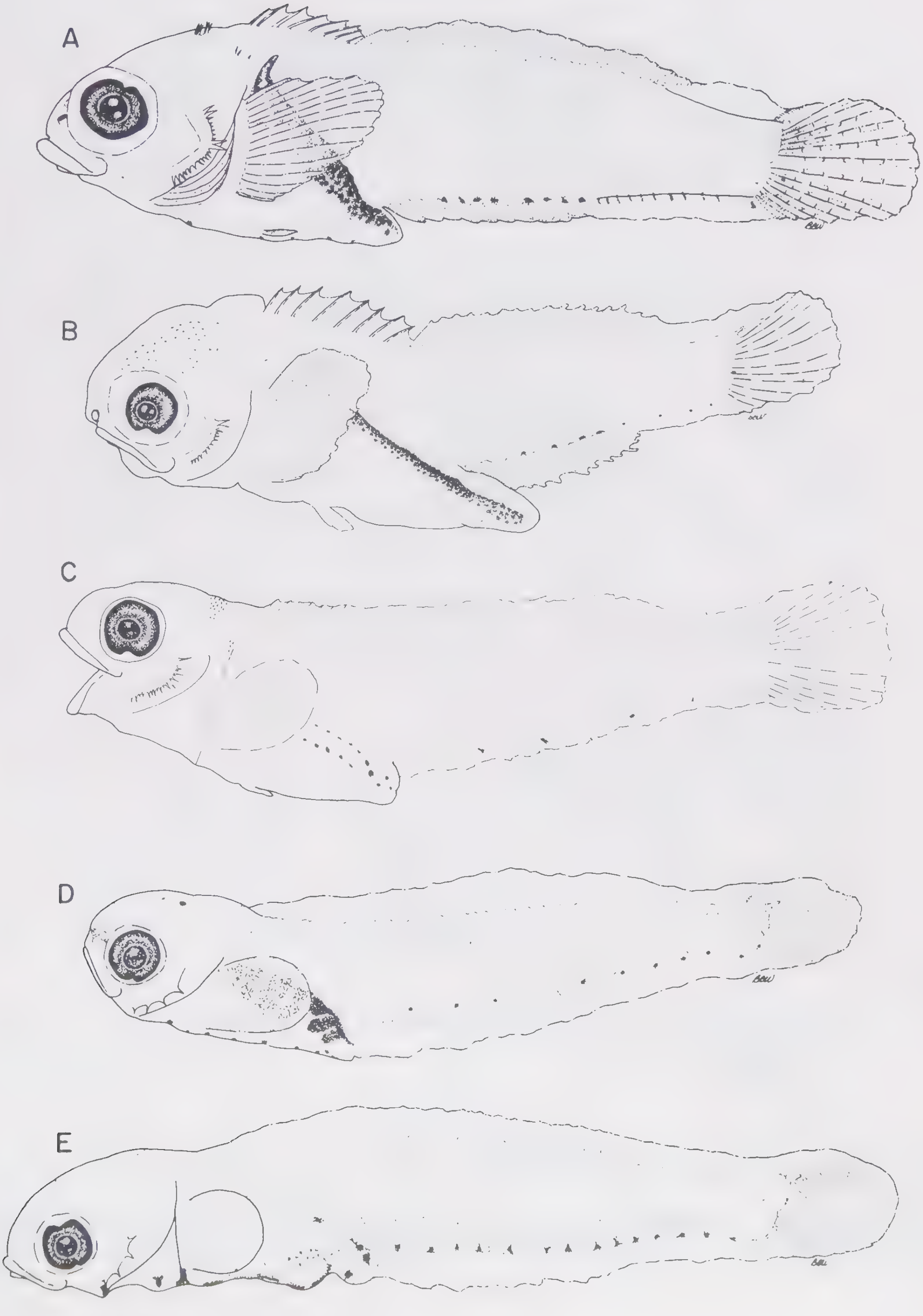
Cottocomephoridae (Fig. 225).—Larvae of seven genera of Lake Baikal cottocomephorids have been described and illustrated (Chernyayev, 1971, 1975, 1978, 1981; Taliev, 1955). Larvae hatch at about 5 to 10 mm, and range from forms with large yolk sacs and no fin development (e.g., *Paracottus*) to well developed, postflexion forms with fins well developed (e.g., *Batrachocottus*). Size at transformation varies from 9 to 20 mm. Larvae are slender with moderately short guts and rounded snouts, somewhat similar to freshwater cottids (*Cottus*) in form. Pigmentation is variable with melanistic pigmentation usually present on the head, nape, gut and variously on the dorsal and ventral midline. Melanophores are frequently present in a row along the lateral midline near the tail tip.

Larvae develop 4 small preopercular spines accompanied by two spiny projections from an inner preopercular shelf. Other head spines are lacking.

Cottidae (Figs. 226–231).—The taxonomic status of the family Cottidae is controversial with the number of recognized families ranging from 1 to 17 (see Washington and Richardson, MS). To minimize confusion, and because there is no generally agreed upon classification of this "family," we use the generic groupings identified by Washington and Richardson (MS) for our discussion of early life history information. Larvae are known for 28 of the 70+ cottid genera. A general overview of larval cottid taxonomy is presented in Richardson and Washington (1980), Richardson (1981a), Washington (1981) and Fahay (1983).

Rhamphocottus (Fig. 226).—Larvae of this distinctive, monotypic species hatch at a relatively large size (6–7 mm NL). Notochord flexion occurs at 7 to 8 mm and transformation to a

Fig. 229. Larvae of the *Artedius* Part A group (A–C) and the *Cottus* group of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Artedius fenestralis,* 9.9 mm SL (from Richardson and Washington, 1980, as *Artedius* Type 2); (B) *Clinocottus acuticeps,* 10.4 mm SL (from Washington, in prep.); (C) *Oligocottus snyderi,* 10.2 mm SL (from Washington, 1981); (D) *Leptocottus armatus,* 8.1 mm SL (from Richardson and Washington, 1980); (E) *Cottus asper,* 8.2 mm SL (ibid.).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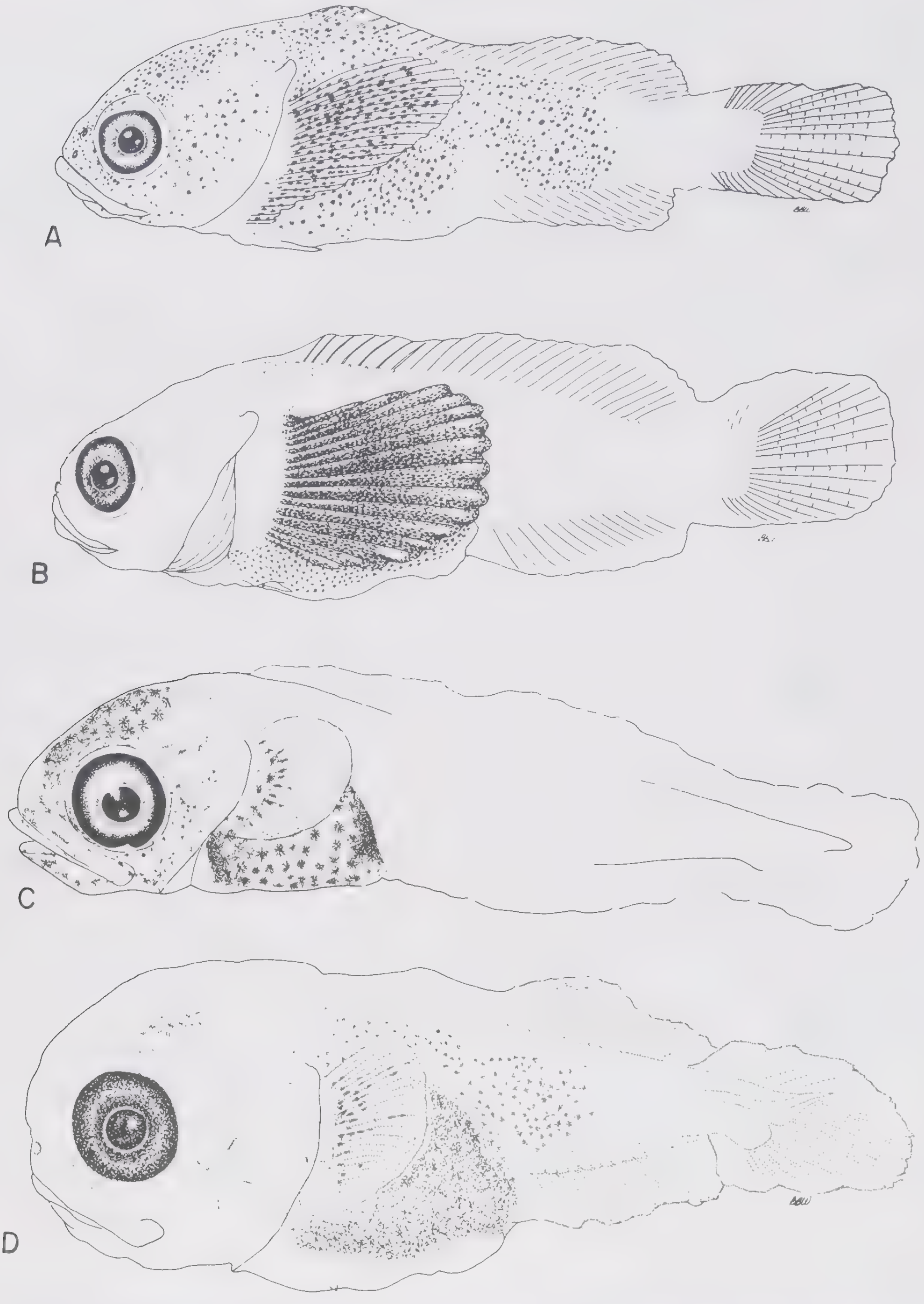

Fig. 230. Larvae of the *Psychrolutes* group (A, B) and the *Malacocottus* group (C, D) of cottids of Washington and Richardson (MS) (see Washington et al., this volume). (A) *Psychrolutes paradoxus*, 13.0 mm SL (from Richardson, 1981a); (B) *Gilbertidia sigalutes*, 13.0 mm SL (ibid.); (C) *Dasycottus setiger*, 10.3 mm SL (original); (D) *Malacocottus zonurus*, 9.8 mm SL (original).

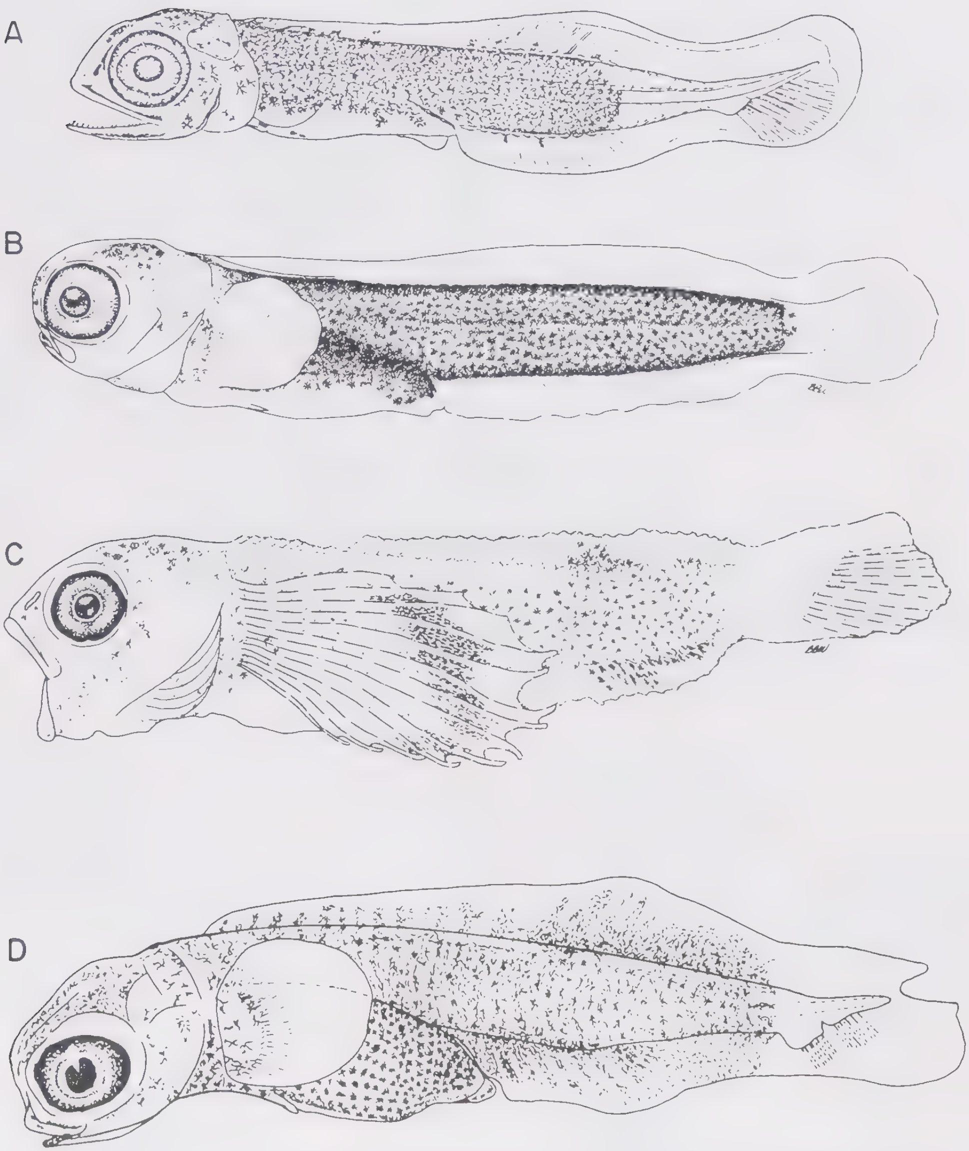

Fig. 231. Larvae of the *Hemitripterus* group (A–C) of cottids of Washington and Richardson (MS) (see Washington et al., this volume) and Agonidae. (A) *Hemitripterus villosus*, ca. 15.5 mm SL (from Kyushin, 1968); (B) *Blepsias cirrhosus*, 11.0 mm SL (from Richardson, 1981a); (C) *Nautichthys oculofasciatus*, 11.7 mm SL (from Richardson and Washington, 1980); (D) *Agonomalus* or *Hypsagonus* sp., 8.2 mm SL (original, courtesy B. Vinter).

benthic juvenile occurs at about 14 to 15 mm SL. *Rhamphocottus* larvae are extremely deep-bodied with a very long snout–anus length.

Larvae are uniformly covered with melanophores except for the caudal peduncle and ventral surface of the gut. *Rhamphocottus* develop small prickle-scales over most of the body by 9 or 10 mm. Larvae develop only one preopercular spine in contrast to the usual four possessed by most cottid larvae. Parietal, nuchal, supracleithral, posttemporal and postocular spines occur during the larval period.

Hemilepidotus-Scorpaenichthys (Fig. 226).—Larvae of this group hatch at 4 to 6 mm NL. Transformation to the neustonic or pelagic juvenile phase occurs at about 13 to 20 mm. Larvae are

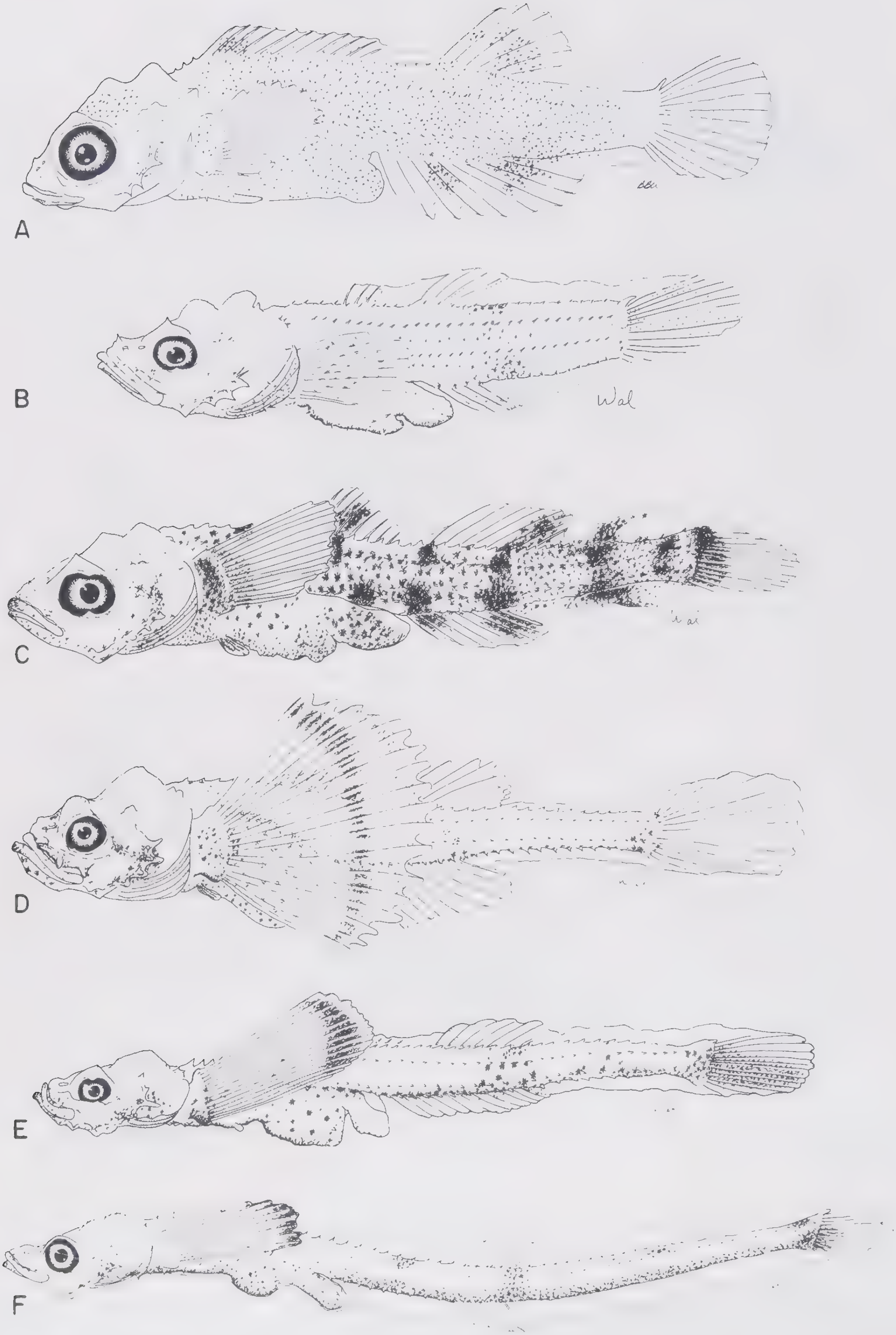

Fig. 232. Larvae of Agonidae (all original). (A) *Hypsagonus quadricornis*, 11.5 mm SL; (B) *Bothragonus swani*, 6.3 mm SL; (C) *Xeneretmus latifrons*, 9.6 mm SL; (D) *Stellerina xyosterna*, 10.2 mm SL; (E) *Ocella verrucosa*, 10.1 mm SL; (F) *Aspidophoroides monopterygius*, 14.3 mm SL.

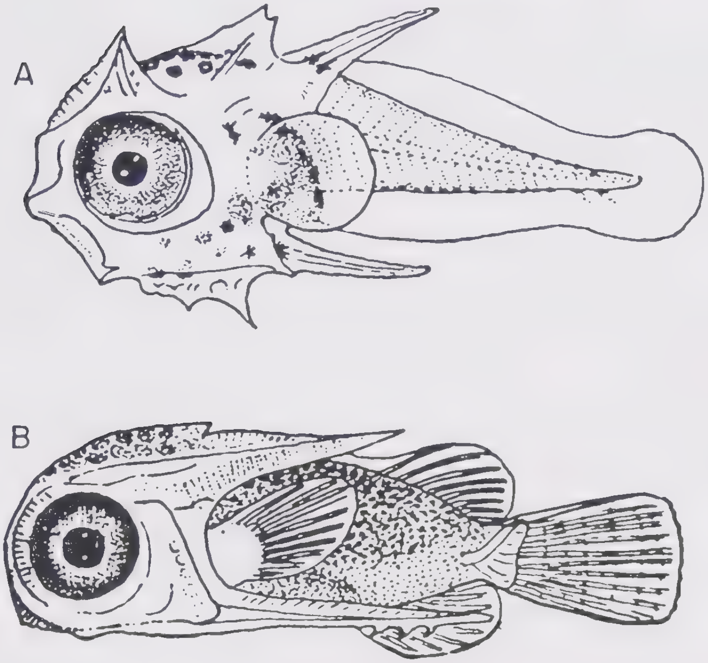

Fig. 233. Larvae of Dactylopteridae. (A) *Dactylopterus volitans*, 2.4 mm (from Padoa, 1956e); (B) *Dactylopterus volitans*, 7.5 mm (ibid.).

long and slender at hatching with moderately long guts (44 to 60%) and rounded snouts. They become increasingly deep-bodied with development.

Larvae are relatively heavily pigmented with melanophores over the head and gut. *Scorpaenichthys* larvae have dense pigment covering the body except for the caudal peduncle while *Hemilepidotus* spp. have postanal pigment concentrated on the dorsal and ventral body midlines. Lateral melanophores develop above and below the notochord in *Hemilepidotus*.

Hemilepidotus and *Scorpaenichthys* larvae develop four prominent preopercular spines. *Hemilepidotus* possess numerous head spines while *Scorpaenichthys* develop bony bumps in corresponding areas. Larvae of this group develop unique pitted dermal bones on the head. In addition, the uppermost pectoral radial is tiny and fuses to the scapula in larval *Scorpaenichthys* and nearly so in *Hemilepidotus*.

Myoxocephalus group (Figs. 227 and 228).—This is the least well-defined and most diverse cottid group containing 13 genera. Where known, size at hatching varies from 2.9 to 10 mm. Transformation to the benthic juvenile stage varies from 7.6 to 20 mm.

Members of this group are generally slender-bodied with pointed snouts; however, *Enophrys* is stout-bodied, and *Orthonopias* has a blunt, rounded snout.

Pigmentation is variable. Heavy pigment on the dorsal surface of the gut, on the nape and along postanal ventral midline is characteristic of many members of this group. Several genera possess heavy melanistic pigmentation on the lateral body surface (e.g. *Radulinus*, some *Myoxocephalus*). Head pigment may be present.

Larvae of this group develop four preopercular spines and a distinctive bony preopercular shelf. Parietal, nuchal, supracleithral, posttemporal and occasionally, postocular spines develop in late-stage larvae.

Artedius group (Fig. 229, Table 107).—This group contains 3 genera, *Artedius* (in part), *Clinocottus* and *Oligocottus* and the larvae have been described by Washington (1981). Larvae hatch at 3 to 5 mm and transform to benthic juveniles at approximately 10 to 13 mm. Larvae are stubby-bodied with a slightly humped appearance at the nape. Snouts are rounded and guts trail distinctively below the ventral body midline. Several species of *Artedius* develop dorsal gut diverticula while *Clinocottus acuticeps* develops long hindgut diverticula.

Larvae are relatively lightly pigmented and characterized by pigment on the nape, over the gut and along the postanal ventral midline. Head pigment is present in some species.

Larvae develop a unique preopercular spine pattern with 6 to 24 spines. Parietal and supracleithral spines are variable in this group and may form in clusters, individually or not at all.

Leptocottus group (Fig. 229).—This group includes the genera *Leptocottus* and *Cottus*. Hatching occurs at 4 to 5 mm and transformation ranges from 8 to 12 mm. Larvae are relatively slender-bodied with rounded snouts and moderately short guts. Pigmentation is usually light with melanophores on the nape, over the gut and widely spaced along the postanal ventral midline. Head pigment may be present.

Where known, these larvae develop four weak preopercular spines; however, other head spines are lacking.

Psychrolutes group (Fig. 230).—This group includes two genera *Psychrolutes* and *Gilbertidia*. Larvae hatch at a relatively large size, about 6 to 7 mm. They transform and settle from the plankton at about 18 to 20 mm SL. Larvae are generally tadpole shaped with large rounded heads tapering toward the tail. Larvae possess an outer layer of loose flabby skin.

Melanistic pigment occurs on the head, nape, gut and characteristically on the pectoral fins. Postanal ventral midline melanophores are absent; however, pigment is added laterally with development.

Head and preopercular spines are absent.

Malacocottus group (Fig. 230).—This group includes *Malacocottus* and *Dasycottus.* Size at hatching is not known. Larvae of this group are similar to those of the *Psychrolutes* group with large, blunt heads tapering to the tail. An outer bubble or layer of skin is present in both genera and is particularly pronounced in *Malacocottus.*

Pigmentation is present on the head, nape and over the entire gut. Pigment occurs laterally on the anterior third of the tail in *Malacocottus* larvae. As in the *Psychrolutes* group, the pectoral fins are characteristically pigmented.

Larvae develop four preopercular spines with a fifth accessory spine present in *Malacocottus.*

Hemitripterus group (Fig. 231).—This group includes the genera: *Hemitripterus, Blepsias* and *Nautichthys.* Hatching occurs at a relatively large size, 7 to 13 mm NL. Newly-hatched larvae have elongate, slender bodies which become deeper with development. *Nautichthys* larvae have distinctively long, pigmented pectoral fins.

Pigmentation is relatively heavy with melanophores covering the head, dorsal surface of the gut and over the lateral body surface except for the caudal peduncle. *Nautichthys* and *Hemitripterus* larvae possess distinctive pigment bands extending onto the dorsal and ventral finfolds that are not found in other cottid larvae.

Larvae develop four prominent preopercular spines and a strong frontoparietal spiny ridge. This group is characterized by delayed ossification in the larval period and a unique "honeycomb" pattern of ossification on the head. *Hemitripterus* larvae develop large bony prickles, similar to the prickle-scales found in agonids.

Agonidae (Figs. 231 and 232).—At least one early life history stage of 9 of the 49 nominal species is known. Agonids hatch at 5.5 to 8.0 mm NL. Development is a gradual transformation to the juvenile form attained at 20 to 30 mm.

Agonid larvae are generally long and slender with relatively long guts. Extremes of form range from short stout genera such as *Agonomalus* and *Bothragonus* to the extremely attenuated forms such as *Ocella* and *Aspidophoroides.* Larvae have distinctively large, fan-shaped pectoral fins.

Pigmentation varies in the family. Melanistic pigment may be present on the head, nape, scattered over the gut and frequently in bands on the postanal lateral surface of the body. The pectoral fins are distinctively pigmented often with distal bands of melanistic pigment. In some species (e.g. *Agonomalus, Hypsagonus*) pigmentation extends onto the dorsal and ventral finfolds.

Larvae are characterized by spiny heads with large frontoparietal spiny ridges, postocular spines, and usually four large preopercular spines. Tiny rows of spines form in small larvae and help distinguish agonid larvae. These rows correspond to the plates (scales) of adults.

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Schindlerioidei: Development and Relationships

W. WATSON, E. G. STEVENS AND A. C. MATARESE

THIS suborder contains a single paedomorphic family composed of two species of the genus *Schindleria.* Both species inhabit neritic surface waters of the subtropical and tropical Indian and Pacific Oceans (Bruun, 1940; Schindler, 1932; R. J. Lavenberg, pers. comm.). Their early life histories are known from the work of Watson and Leis (1974), Miller et al. (1979), and Ozawa and Matsui (1979). Classification of Schindlerioidei is speculative, and its placement here by Nelson (1976) follows Gosline (1971), who tentatively considered this taxon a percoid derivative, possibly related to Ammodytoidei.

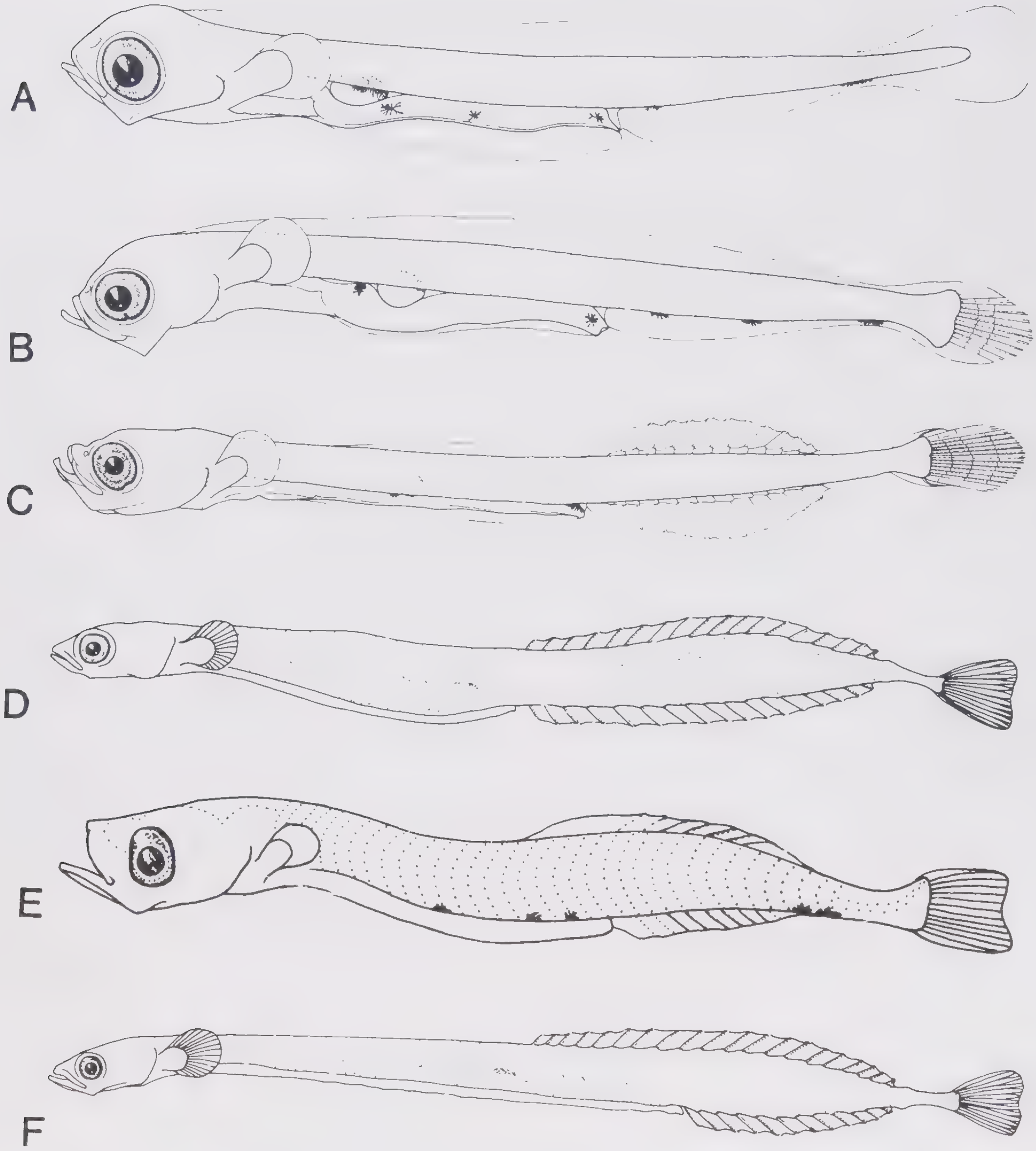

Fig. 298. Lateral views of: (A) *Schindleria pietschmanni* larva, 2.7 mm; (B) *S. pietschmanni* larva, 3.5 mm (redrawn from Miller et al., 1979); (C) *S. pietschmanni* larva, 4.7 mm (from Miller et al., 1979); (D) *S. pietschmanni* adult female, 15.1 mm (redrawn from Jones and Kumaran, 1964); (E) *S. praematura* larva, 3.6 mm (from Ozawa and Matsui, 1979); and (F) *S. praematura* adult female, 20.1 mm (redrawn from Jones and Kumaran, 1964).

DEVELOPMENT

Eggs

Although ovarian eggs are well-known for both species (Jones and Kumaran, 1964; Sardou, 1974), the mode of spawning is unknown. Watson and Leis (1974) reported planktonic *Schindleria* sp. eggs which they suggested were either pelagic or perhaps dermersal eggs extruded in the net. The largest ovarian eggs lack oil droplets and are irregular in shape, 0.35–0.40 mm in diameter (*S. praematura*), or oval, 0.30 × 0.65 mm (*S. pietschmanni*). Hydrated, planktonic eggs of *Schindleria* sp. are oval, 0.50 × 1.30 mm, contain no droplets, and have an unsculptured chorion with a cap-like structure at one end. Incubation time is not known.

Larvae

Morphology.—Larval size and degree of development at hatching are unknown. However, *S. pietschmanni* at 1.9 mm NL has a rather large yolk sac (containing an apparently segmented yolk) in addition to pigmented eyes and an open, presumably functional, mouth. Notochord flexion occurs after 2.7 mm but before 3.5 mm NL in *S. pietschmanni,* and before 4.3 mm in *S. praematura.* Development to the essentially larval mature form is gradual. The juvenile stage may be taken to begin with completion of the dorsal and anal fins and the acquisition of the principal caudal rays (ca. 4–5 mm), and the adult stage to begin when the male genital papilla or the ovaries of the female become discernable (longer than ca. 9 mm SL). The distinctive schindleriid terminal section at the rear of the vertebral column does not become apparent until the late larval or early juvenile period.

Aside from fin development, morphology changes little during larval development. The swim bladder moves posteriorly from myomeres 6–8 to myomeres 14–15 in *S. pietschmanni*; a similar migration presumably occurs in *S. praematura* (e.g., Sardou, 1974). Preanal length is greater in *S. praematura* than in *S. pietschmanni.*

Pigmentation.—Schindleriids are lightly pigmented throughout development (e.g., Miller et al., 1979; Ozawa and Matsui, 1979). During the larval and early juvenile period, *S. pietschmanni* has one to four pairs of melanophores along the sides of the gut (usually two or three pairs), one to four melanophores along the ventral midline of the tail (usually two or three), and pigment on the posterior dorsal surface of the swim bladder. The posterior tail melanophore is typically more elongate than the others (Fig. 298). All but the swim bladder pigment is lost during the juvenile stage. Larval pigmentation of *S. praematura,* as shown by Ozawa and Matsui (1979), and juvenile pigment, shown by Sardou (1974), are very similar to that of *S. pietschmanni.* Like *S. pietschmanni, S. praematura* retains only the posterior swim bladder pigment in the adult stage (Fig. 298).

Meristics.—Meristics for *Schindleria* are: Vertebrae 15–25 + 12–21 = 33–44; D 15–22; A 10–14; P 15–17; and C 13 prin. A combination of caudal vertebrae and anal fin ray counts usually will distinguish the two species.

The caudal fin rays are the first to develop, followed by the dorsal and anal fin rays (forming simultaneously). Pectoral fin rays are the last to ossify. Pelvic fins never form.

RELATIONSHIPS

Early life history characters, to the extent that they are presently known, do little to clarify the phylogenetic position of the Schindlerioidei. For example, Gosline (1963b, 1971) speculated that Schindlerioidei might be derived from an ammodytoid ancestor; however, while both suborders share some characters (e.g., an elongate larval form with preanal length just over 50% body length), they differ in other important ways (e.g., late development of pectoral fin rays in schlindleriids and early development in ammodytoids). Knowledge of spawning and early development might aid in ascertaining schindleriid relationships although at present this group seems destined to remain an enigma.

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Trachinoidea: Development and Relationships

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THE blennioid infraorder Trachinoidea, as used here, contains about 140 species in 11 families of morphologically quite diverse, but generally small, primarily shallow-living temperate and tropical marine demersal or burrowing fishes (Chiasmodontidae is bathypelagic; Cheimarrhichthyidae inhabits fresh water). These families have not always been considered as closely related (e.g., Gosline, 1968, 1971), but we follow Nelson (1976) in considering them together here. Nelson (1976) originally placed 16 families in the Trachinoidea, but subsequently synonymized the Limnichthyidae with Creediidae (Nelson, 1978). Springer (1978) removed Oxudercidae to the Gobiidae. Three other families are treated elsewhere in this volume: Bathymasteridae and Dactyloscopidae with the Blennioidea (Matarese et al., this volume) and Opistognathidae with the Percoidei (G. D. Johnson).

In this brief review, we summarize the present state of knowledge of the early life histories of trachinoid fishes and attempt to determine whether such information contributes to our understanding of their phylogenetic relationships. Unfortunately, early life histories, mostly incomplete, are known for only a small number of species (Table 134). This paucity of early life history data makes generalizations about development tenuous at best, but for purposes of this paper the known taxa are considered representative.

Development

Eggs

Eggs are unknown for the Percophididae, Trichonotidae, and Leptoscopidae. Only ovarian eggs have been described for the

Table 134. Summary of Early Life History Information Available for Trachinoid Fishes.

Family	Number of genera	Approximate number of species	Distribution	Descriptions		Illustrations		Early life history source
				Genera	Species	Genera	Species	
Trichodontidae	2	2	North Pacific	1	1	1	1	Breder and Rosen, 1966; Marliave, 1981
Champsodontidae	1	10	Indo-Pacific	1	1	1	1	Mito, 1962d, 1966
Chiasmodontidae	4	23	Worldwide (temperate and tropical, marine)	1	1	1	1	Ahlstrom, pers. comm.; Lavenberg, pers. comm.
Percophididae	6	17	Atlantic, Indo-Pacific	1	1	1	1	Crossland, 1982
Mugiloididae	3	36	Atlantic, Indian, Pacific (subtropical and tropical)	1	5	1	4	Leis and Rennis, 1983; Mito, 1966; Robertson, 1973, 1975a; Watson, unpubl.
Trichonotidae	2	5	Indo-Pacific	1	2	1	1	Leis and Rennis, 1983
Cheimarrhichthyidae	1	1	New Zealand (freshwater)	0	0	0	0	McDowall, 1973c
Creediidae	7	14	Indo-Pacific	2	2	2	3	Leis, 1982; Leis and Rennis, 1983; Regan, 1916; Watson and Leis, 1974
Trachinidae	1	4–5	Eastern Atlantic, Mediterranean	1	4	1	2	Breder and Rosen, 1966; Dekhnik, 1973; Ehrenbaum, 1905–1909; Marinaro, 1971; Padoa, 1956g; Russell, 1976; Schnakenbeck, 1928; Vodyanitsky and Kazanova, 1954
Uranoscopidae	8	25	Atlantic, Indian, Pacific (shallow temperate and tropical)	3	4	2	3	Dekhnik, 1973; Fritzsche, 1978; Mito, 1966; Robertson, 1974
Leptoscopidae	2	3	Australia, New Zealand (marine)	0	0	0	0	

Cheimarrhichthyidae (McDowall, 1973c). Six of the seven remaining families spawn small to moderate (0.70–2.45 mm diameter), spherical, single pelagic eggs (Table 135). McDowall (1973c) suggested a pelagic spawning mode for Cheimarrhichthyidae as well, unusual for the suggested riparian spawning habitat but consistent with the close relationship, or identity, of Cheimarrhichthyidae with Mugiloididae. All pelagic eggs have oil droplets (most have only one, 0.16–0.26 mm in diameter) and all except some Uranoscopidae have smooth, unsculptured chorions. Incubation periods range from 2 to 6 days and larvae are not well developed at hatching (Trachinidae are somewhat better developed, with pigmented eyes and pelvic buds).

Demersal egg masses (750–1,000 eggs) are produced only by the Trichodontidae (Table 135). These eggs are large (3.52 mm in diameter), slightly flattened, with an unsculptured chorion and no oil droplet. Incubation is estimated at about one year (Marliave, 1981) and larvae are well developed at hatching.

Larvae

Larval stages are unknown for the Cheimarrhichthyidae and Leptoscopidae. The described trachinoid larvae display only a few unifying characteristics: (1) all are pelagic, hatching at ca. 2–15 mm (Table 136); (2) they pass through no specialized stages (except the gargaropteron juvenile stage of the chiasmodontid genus *Kali*); and (3) they metamorphose gradually to the demersal juvenile stage at a small to moderate size (ca. 10–60 mm).

Morphology.—Morphology is quite variable; however, larvae are either relatively long and slender (Fig. 299: Trichodontidae, Chiasmodontidae, Percophididae, Trichonotidae, Creediidae) or rather robust (Fig. 300: Champsodontidae, Mugiloididae, Trachinidae, Uranoscopidae). All the robust larvae and one of the slender types (Trichodontidae) have somewhat rounded heads with relatively short snouts. Preanal length in both types usually is not more than 50% of standard length (60% or more in Creediidae and Trichonotidae) and changes little during development. Head and body spination are extremely variable. Preopercular spination is known for six families: Trichodontidae, Chiasmodontidae, Champsodontidae, Mugiloididae, Creediidae, and Trachinidae. Champsodontid larvae develop a serrate crest on the snout and head during the postflexion period, and chiasmodontid larvae (except *Kali*: R. J. Lavenberg, pers. comm.) develop small body spicules (Fig. 299) just before or during notochord flexion.

Pigmentation.—Pigmentation of trachinoid larvae is quite variable, from nearly absent to quite intense (Table 137). Larval champsodontids, mugiloidids, trichonotids, and creediids remain lightly pigmented throughout development, while larval trichodontids, chiasmodontids, trachinids, and uranoscopids may become rather heavily pigmented. Pigmentation usually increases with increasing larval size; trichonotids and creediids change little in pigmentation with growth.

Head.—Eyes are pigmented at hatching for the demersally-spawned Trichodontidae, and for two of the six families with pelagic eggs (Table 137). Pigmentation is present at hatching, or subsequently develops, over the brain in five families. The degree of pigmentation of other areas of the head is variable.

Gut.—Pigmentation typically is present dorsally over the gut and swim bladder throughout larval development (absent only in creediids and postflexion trichonotids). Other gut pigment is variable.

TABLE 135. CHARACTERISTICS OF TRACHINOID EGGS.

Family	Pelagic (P) or demersal (D)	Single or mass	Egg diameter (mm)	Oil droplets number: size range (mm)	Attachments or ornamentation	Pigmentation	Incubation period	Source
Trichodontidae	D	Mass 750–1,000 eggs	3.52	0	None	Amber	2 mo.–1 yr.	Breder and Rosen, 1966; Marliave, 1981
Champsodontidae	P	Single	1.09–1.19	1: 0.17–0.22	None	Melanophores on embryo and oil droplet		McDowell, 1973c; Mito, 1966
Chiasmodontidae	P	Single	1.08–1.14	1: 0.26	None	Chorion rose to amber		Ahlstrom, pers. comm.
Percophididae	Unknown							
Mugiloididae	P	Single	0.77–1.25	1: 0.16–0.25	None	Melanophores on embryo and oil droplet	5–6 days	Mito, 1966; Robertson, 1973, 1975a
Trichonotidae	Unknown							
Cheimarrhichthyidae	P (assumed)	Single (ovarian)						McDowell, 1973c
Creediidae	P	Single	0.70–1.10	400–600 in 8–12 clusters; coalesce to 3–8: 0.05–0.10	None	Melanophores on embryo	2 days	Leis, 1982; Watson and Leis, 1974
Trachinidae	P	Single	0.94–1.37	1–30, coalesce: 0.19–0.25	None		4–5 days	Breder and Rosen, 1966; Dekhnik, 1973; Marinaro, 1971; Padoa, 1956g; Russell, 1976
Uranoscopidae	P	Single	1.52–2.45	3–27: 0.02–0.15	Polygonal network on chorion in *Uranoscopus*	Melanophores on yolk and embryo		Dekhnik, 1973; Fritzsche, 1978; Mito, 1966; Robertson, 1975a
Leptoscopidae	Unknown							

Trunk and tail.—Most trachinoid larvae display some degree of pigmentation along the ventral margin of the tail (absent in some mugiloidids and preflexion trachinids). Pigmentation (typically rather light) occurs along the dorsal margin of the trunk and tail at some time during larval development in many trachinoids. Internal pigment may develop above and below the vertebral column (e.g., Trichodontidae).

Hypural margin.—Hypural pigment typically is light or absent although its presence as a bar is diagnostic for the Trichodontidae.

Fins.—Fins typically are unpigmented in trachinoid larvae, although for some groups fin pigmentation can be diagnostic (e.g., the caudal and posterior dorsal and anal fin pigment of Trich-

TABLE 136. SIZE (MM SL) OF TRACHINOID LARVAE AT SELECTED DEVELOPMENTAL STAGES.

Family	Hatching	Notochord flexion	Prejuvenile or specialized stages	Juvenile
Trichodontidae	14.5	Before hatching	None	32–60
Champsodontidae	3.4–3.7	4.6–5.0	None	9.6–10.7
Chiasmodontidae	ca. 4	Before ca. 9	ca. 45	ca. 12–45
Percophididae		<16.0		
Mugiloididae	2.2–3.0	3.7–4.8	None	10.0 to ≥12.6
Trichonotidae		5.2–6.3	None	>18.8
Cheimarrhichthyidae				≤25
Creediidae	2.6–3.5	7.0–10.2	None	>11.0, ≤29.2
Trachinidae	3.2	5.0–10.0	None	13–15
Uranoscopidae	≥2.5–4.38		None	≥23
Leptoscopidae	No information			

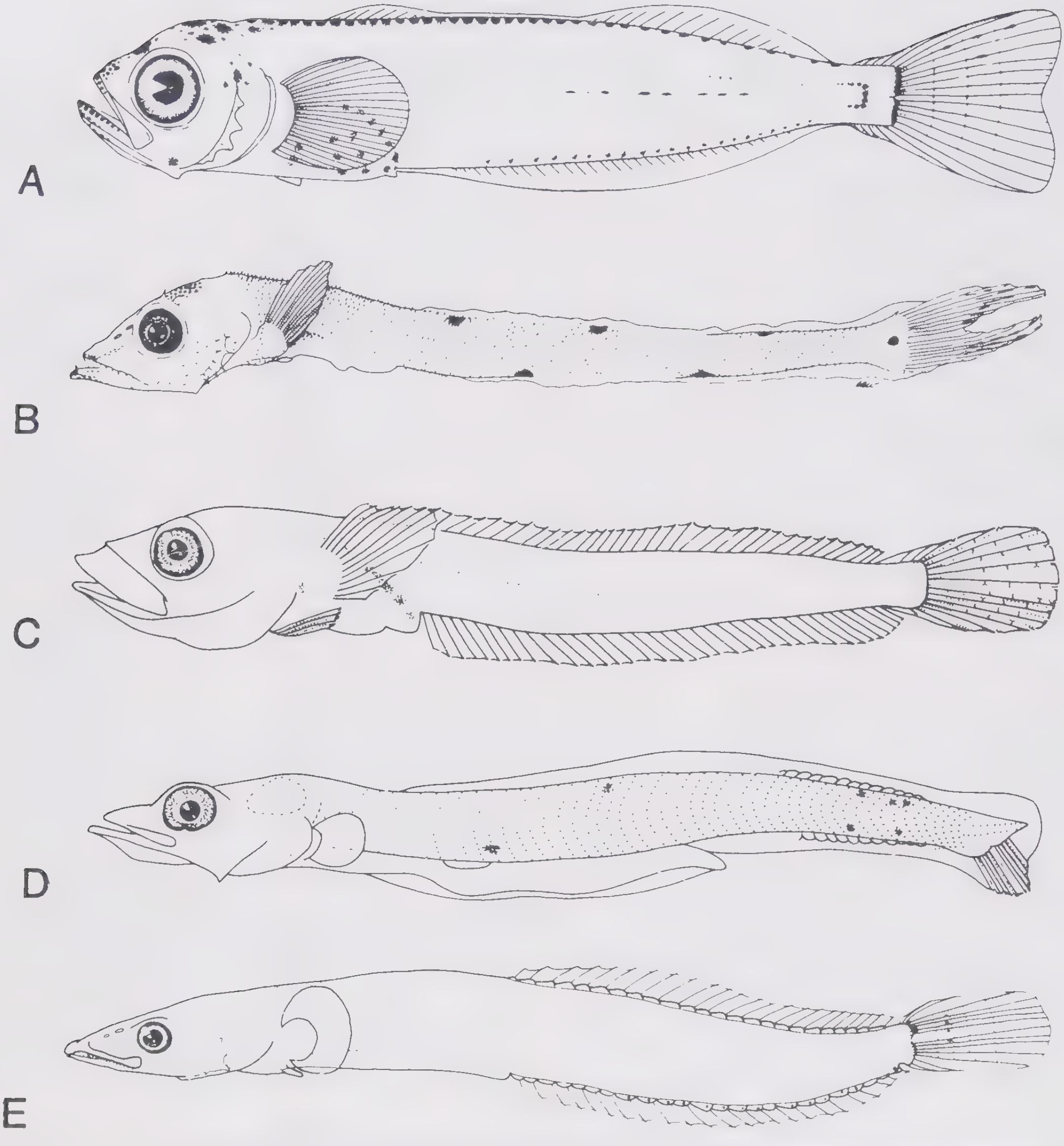

Fig. 299. (A) Trichodontidae: *Trichodon trichodon*, 13.0 mm, from Marliave (1981); (B) Chiasmodontidae: *Pseudoscopelus* sp., 14.0 mm, CalCOFI station 5710-5-130.80 (approximately 24°49′N, 116°49′W); (C) Percophididae: *Hemerocoetes* sp., 16.0 mm, redrawn from Crossland (1982); (D) Trichonotidae: *Trichonotus* sp., 5.9 mm, from Leis and Rennis (1983); and (E) Creediidae: *Limnichthys donaldsoni*, 11.0 mm, from Leis (1982).

onotidae or the early developing heavily pigmented pelvic fins of trachinids).

Meristic characters.—Vertebral and fin ray counts are summarized in Table 138. The sequence of fin ray formation, incompletely described for most families, appears to be quite variable except that the caudal fin is first to begin ossification of rays in all but the trachinids (the caudal is second in this family, following the pelvic fins). Dorsal and anal fin rays are second to form in four families (Mugiloididae, Trichonotidae, Creediidae, Uranoscopidae), while pectoral fin rays are second in two (Trichodontidae and Chiasmodontidae) and pelvic fin rays in one (Champsodontidae).

Special structures.—Special structures are generally lacking in trachinoid larvae. Only the elongate opercular appendage of

TABLE 137. SUMMARY OF PIGMENTATION (MELANIN ONLY) OF LARVAL TRACHINOID FISHES. Key: +, present; 0, absent; ↑, increasing with development; ↓, decreasing with development; 0→+, initially unpigmented, becoming pigmented with development; An, anterior; Po, posterior.

		Head						Gut				Trunk and tail Ventral margin	
Family	Eye at hatching	Brain	Jaws	Snout	Opercle	Isthmus	Nape	Anterior	Dorsal	Ventral	Lateral	Preflexion	Flexion
Trichodontidae	+	+↑	+	+	0	0	0→+	0	0	0	+		+
Champsodontidae	+	+	0	+↓	0	0	0→+	0	+	0→+	+	+	+
Chiasmodontidae	0	+	+	0	0	0→+	0	0	+	0	0	+	+
Percophididae		0	0	0	+	0	0	0	+	0	0		
Mugiloididae	0	0, or +↓, or +↑	0	0, or +↓	0	0	0	0, or +	+↑	0, or +	0→+	0, or +	+
Trichonotidae	0	0	0	0	0	0	0	0	+↓	0	0	+ Po	+ Po
Cheimarrhichthyidae[1]													
Creediidae	0	0	0	0	0	0	0	0	0	+	0	+ Po	+ Po
Trachinidae	+	0, or +↑	0, or +↑	0, or +↑	0→+↑	0	0, or +	0	+	0	0→+↑	0, or +	+
Uranoscopidae	0	+↑	0→+	+↑	0→+	0→+	0→+	+	+↑	0→+↑ or +↑	0→+↑ or +↑	+↑, or +↓	+↑, or +↓
Leptoscopidae[1]													

[1] Larvae unknown

TABLE 138. SELECTED MERISTICS OF TRACHINOID FISHES.

Family	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Primary caudal fin rays	Vertebrate	Source
Trichodontidae	X–XVI + 0–I, 13–19	I, 27–31	21–23	I, 5	12–15	12–15 + 34–40 = 47–50	Marliave, 1981; NWAFC, unpubl.
Champsodontidae	V + I, 18–22	I, 17–20	9–13	I, 5		10 + 19–22 = 29–32	de Beaufort and Chapman, 1951; Matsubara et al., 1964; Mito, 1962d
Chiasmodontidae	VI–XIII + 18–28	0–I, 17–28	10–15	I, 5	17	33–44	Johnson and Cohen, 1974; Lavenberg, pers. comm.; Norman, 1929
Percophididae	0–IX + 14–31	0–I, 15–42	20–28	I, 5	15	8–9 + 19–21 = 27–30	Ginsburg, 1955; Iwamoto and Staiger, 1976; Miller and Jorgenson, 1973
Mugiloididae	IV–VII, 19–28	I, 16–26	15–22	I, 5	14–15	10–16 + 18–22 = 28–38	Cantwell, 1964
Trichonotidae	III–VII, 40–46	36–40	12–14	I, 5	13	15 + 40 = 55	Leis and Rennis, 1983; Masuda et al., 1975
Cheimarrhichthyidae	IV–VI, 18–21	I–II, 14–16	14–18	I, 5	12–15	12 + 20–21 = 32–33	McDowall, 1973c
Creediidae	18–40	25–40	11–17	None, or I, 3–5	10	37–59	Leis and Rennis, 1983; Smith, 1961
Trachinidae	V–VII + 21–32	25–36	15	I, 5	14	11–12 + 23–31 = 34–43	Padoa, 1956g; Russell, 1976
Uranoscopidae	0–V + 12–19	0–I, 12–19	13–24	I, 5	11–14	9–12 + 14–17 = 25–29	Berry and Anderson, 1961; Fritzsche, 1978; Marshall, 1965; Miller and Jorgenson, 1973; Mito, 1966; Scott et al., 1974; Smith, 1961; Wade, 1946
Leptoscopidae	34–35	37		I, 5		10+	Gosline, 1968; Scott et al., 1974

TABLE 137. EXTENDED.

Trunk and tail							Fins							
Ventral margin	Dorsal margin			Lateral										
Post-flexion	Pre-flexion	Flexion	Post-flexion	Pre-flexion	Flexion	Post-flexion	Hypural margin	Dorsal	Anal	Pec-toral	Pelvic	Caudal	Source
+		0→+ An	+↑		0	+↑	+	0→+	0	0→+	0	0→+	Marliave, 1981
+	+	+	+	0	0, or +	0, or +	0	+↓	+↓	0	0	+↓	Mito, 1962d, 1966
+	0, or +	0, or +	+	0	0	0	0	0	0	0	0	0	Ahlstrom, pers. comm.; Lavenberg, pers. comm.
0			0			0		0	0	0	0	0	McDowall, 1973c
+, or +↓	+↓ Po	0, or +↓ Po	0	0, or + Po	0, or + Po	0, or + An	0	0	0	0, or +	0, or +	0	Leis and Rennis, 1983; Mito, 1966; Robertson, 1973; Watson, unpubl.
+ Po	+ Po	+ Po	+ Po	+ Po	+ Po	+ Po	0	+ Po	+ Po	0	0	+	Leis and Rennis, 1983
+ Po	+ Po	+ Po	0, or + Po	0	0	+	0→+	+↓ Po	+↓Po	0	0	+	Leis, 1982; Leis and Rennis, 1983; Regan, 1916
+	0, or + An	0, or + An	0, or + An	0	0, or + An	+ An	+	0→+↑	0	0	+	0	Ehrenbaum, 1905–1909; Padoa, 1956g; Russell, 1976
0, or +	+	0	0	+	+ An	+	+	0, or +↓	0, or +↓	0	0	0	Dekhnik, 1973; Mito, 1966; Pearson, 1941

Champsodon, and the body spicules of the chiasmodontids (except *Kali*) are distinctive. *Trachinus vipera* has precocious, enlarged, and heavily pigmented pelvic fins.

RELATIONSHIPS

The trachinoid families summarized here are presumed to be derived from the Percoidei, or in some cases to belong themselves to the Percoidei (e.g., Trichodontidae, Champsodontidae, Chiasmodontidae: Gosline, 1971). Therefore, in the following discussion we consider early life history characters shared with the Percoidei as primitive. Characters shared with other Blennioidei are, somewhat arbitrarily, considered to be derived. Our purpose in classifying characters into these categories is not to develop a new phylogeny of the Trachinoidea based on early life history, since far too little in known to allow such an undertaking, but rather to determine whether such characters support our treatment of the Trachinoidea as a monophyletic group.

Six of the 11 trachinoid families retain the pelagic spawning

TABLE 139. SUMMARY OF EARLY LIFE HISTORY CHARACTERISTICS OF THE TRACHINOIDEA. The percoid condition is assumed to be primitive, while the blennioid condition is assumed to be derived. The percoid condition includes spawning of pelagic eggs which soon hatch to poorly-differentiated larvae, a moderately deep body, myomeres mid-to-upper twenties, development of dorsal and anal fin rays before pectoral and/or pelvic fin rays, and five pelvic fin rays. The blennioid condition includes spawning of non-pelagic eggs with an extended incubation period and hatching of well developed larvae having pigmented eyes, an elongate shape, myomeres thirty or more, development of pectoral and/or pelvic fin rays before dorsal and anal fin rays, and fewer than five pelvic fin rays. It should be understood that spawning mode, incubation period and development at hatching tend to be correlated, as are larval shape and number of myomeres.

	Eggs			Larvae					
Family	Spawning mode	Incubation period	Development at hatching	Larval shape	Number of myomeres	Pectoral pelvic fin ossification	Reduced number of pelvic rays	Pre-opercular spination	Larval pigmentation
Trichodontidae	Derived	Derived	Derived	Derived	Derived	Derived	Primitive	Present	Heavy
Champsodontidae	Primitive		Derived	Primitive	Primitive	Derived	Primitive	Present	Light
Chiasmodontidae	Primitive		Primitive	Derived	Derived	Derived	Primitive	Present	Heavy
Percophididae				Derived	Primitive	Primitive	Primitive	Absent	Light
Mugiloididae	Primitive	Derived	Primitive	Primitive	Primitive	Primitive	Primitive	Present	Light
Trichonotidae				Derived	Derived	Primitive	Primitive	Absent	Light
Cheimarrhichthyidae	Primitive?								
Creediidae	Primitive	Primitive	Primitive	Derived	Derived	Primitive	Derived	Present	Light
Trachinidae	Primitive	Derived	Derived	Primitive	Derived	Derived	Primitive	Present	Heavy
Uranoscopidae	Primitive		Primitive	Primitive	Primitive	Primitive	Primitive	Absent	Heavy
Leptoscopidae									

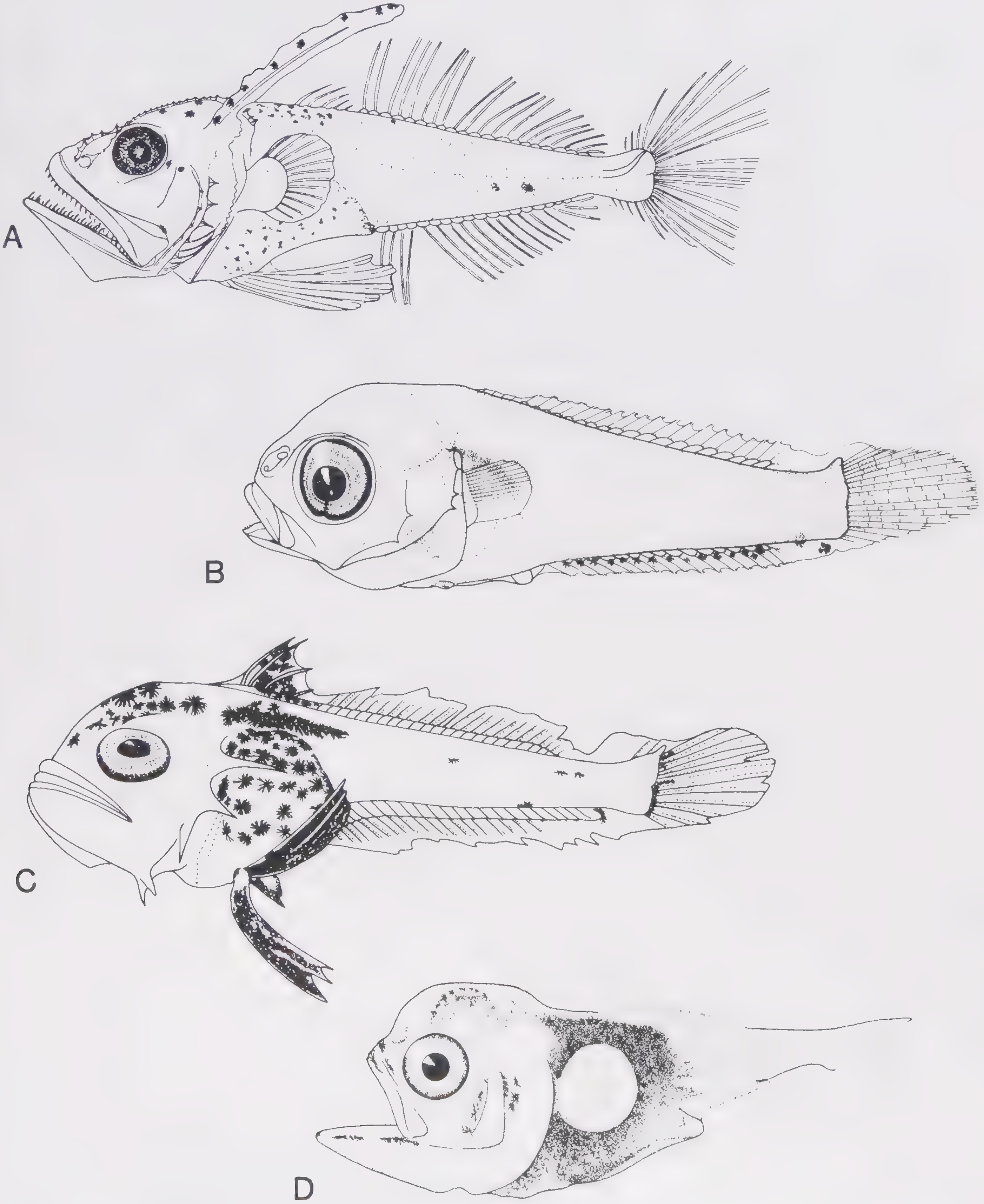

Fig. 300. (A) Champsodontidae: *Champsodon snyderi*, 9.6 mm, from Mito (1962a); (B) Mugiloididae: *Parapercis schauinslandi*, 5.3 mm, Kahe Point, Oahu, Hawaii (approximately 21°16'N, 158°5'W); (C) Trachinidae: *Trachinus vipera*, 7.5 mm, redrawn from Schnakenbeck (1928); and (D) Uranoscopidae: *Astroscopus guttatus*, 4.9 mm, from Pearson (1941).

mode (Tables 135 and 139) typical of the marine percoids, one shares with the other Blennioidei the condition of spawning nonpelagic egg masses. Among the pelagic spawners, four retain the percoid-like condition of early hatching of poorly-differentiated larvae; two share with the demersal spawners the condition of a relatively long incubation and hatching of well developed larvae with pigmented eyes.

The larvae of four families are moderately deep-bodied, a character shared with the majority of percoids. Each of these families (except Trachinidae) contains at least some species with myomeres numbering in the mid-to-upper twenties: typical percoid counts. Five trachinoid families resemble blennioids in having elongate larvae, usually with more than 30 myomeres.

All trachinoid larvae (except some Trachinidae) follow the typical perciform pattern of beginning caudal fin ossification first; larvae of five families follow the percoid pattern of beginning ossification of dorsal and anal fin rays before pectoral and pelvic fin rays. Four families share with the other blennioids the early acquisition of pectoral and/or pelvic fin rays. All trachinoid families share with the other blennioids the jugular placement of pelvic fins, but only one family (not all species) also shares the blennioid condition of fewer than five pelvic fin rays.

Larval pigmentation and preopercular spination of the Trachinoidea (Table 139) are difficult to assess, since both range from absent to highly developed in both the Percoidei and Blennioidei. The distribution of these characters is listed in Table 139 to aid in determining relationships among the Trachinoidea.

Based solely on early life history characters (Table 139), the Uranoscopidae and Mugiloididae (including Cheimarrhichthyidae?) appear to be the most percoid-like members of the Trachinoidea, while Trichodontidae are most like the other Blennioidei. Two points become clear in considering the contribution of early life history to the understanding of trachinoid phylogeny: (1) the Trachinoidea is a very diverse, probably polyphyletic, group; and (2) much more early life history data are needed before any substantial contribution can be made to the understanding of this group.

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